BIOMETRIC AND EDDY-COVARIANCE ESTIMATES OF ECOSYSTEM CARBON STORAGE AT TWO BOREAL FOREST STANDS IN SASKATCHEWAN: 1994-2004

A Thesis Submitted to the College of
Graduate Studies and Research
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in the Department of Soil Science
University of Saskatchewan
Saskatoon

By

Alison Deanne Theede

PERMISSION OF USE

In presenting this thesis in partial fulfilment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Soil Science
University of Saskatchewan
Saskatoon, Saskatchewan S7N 5A8

ABSTRACT

The boreal forest is one of the world's largest forest biomes and comprises a major portion of the terrestrial carbon (C) sink. Quantifying the net C change in forest ecosystems is an important step in understanding and modeling the global C cycle. The goals of this project were: to estimate and compare the total change in ecosystem C over a 10-year period in two boreal forest stands using biometric and eddy-covariance approaches, and to evaluate the year-to-year changes in C uptake. This study utilized 10 years of eddy-covariance data and *ecosys* model data from the Old Aspen (OA) and Old Jack Pine (OJP) sites in central Saskatchewan, part of the Boreal Ecosystem Research and Monitoring Sites (BERMS). According to the eddy-covariance and C stock approaches, between 1994 and 2004 the net change in C storage at OA was 15.6 ± 4.0 and 18.2 ± 8.0 Mg C ha^{-1}, respectively. At OJP, the 10-year net change in C storage from eddy-covariance was 5.8 ± 2.0 Mg C ha^{-1} in comparison to 6.9 ± 1.6 Mg C ha^{-1} from the carbon stock approach. While both sites were sinks of C between 1994 and 2004, the greatest increase in C occurred in different components - the forest floor at OA (14.6 Mg C ha^{-1}) and in the living vegetation at OJP (8.0 Mg C ha^{-1}). In 2004, total ecosystem C content was greater at OA (180.6 Mg C ha^{-1}) than OJP (78.9 Mg C ha^{-1}), with 50% (OA) and 39% (OJP) of the C in the detritus and mineral soil pools. During the 10-year period of eddy-covariance measurements, there was a positive correlation between both annual and growing season gross ecosystem photosynthesis (GEP) and live stem C biomass increment at OA, whereas no significant relationships were found at OJP. Stem C increment accounted for 30% of total net primary productivity (NPP) at both sites, and NPP/GEP ratios were 0.36 and 0.32 at OA and OJP, respectively. Overall, this study found good agreement between eddy-covariance and biometric estimates of ecosystem C change at OA and OJP between 1994 and 2004. Over that period at OA, eddy-covariance estimates of photosynthesis captured the inter-annual variability in C uptake based on the growth of tree rings.

ACKNOWLEDGEMENTS

I would like to acknowledge Dr. Alan Barr and Dr. Darwin Anderson for their knowledge and support throughout this project. Your input and guidance was invaluable. Thank you to my advisory committee, Dr. Ted Hogg and Dr. Ken Van Rees who have been extremely supportive throughout this project making their time, expertise, and lab resources available to me. I also want to thank my external examiner Dr. Jeff Thorpe for his suggestions and comments. Thank you to Kim Kovacs, Courtney Campbell and Kristin Sheppard for all their hard work in the field. Thank you as well to the department of Soil Science and fellow grad students for their friendship and support.

This research was supported by the Fluxnet Canada Research Network through funding from BIOCAP Canada, the Canadian Foundation for Climate and Atmospheric Sciences (CFCAS) and the Natural Sciences and Engineering Research Council of Canada (NSERC).

A very special thank you to Geoff for his love, support and encouragement. Thanks to Dade for his bright smile, wonderful imagination and endless energy. Thank you to my family and the Meinert family for their unconditional love and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Forests worldwide have been the focus of much research because of the critical role they play in the global carbon (C) cycle. Forest ecosystems comprise a major portion of the terrestrial C sink and help regulate C cycling between the terrestrial ecosystem and the atmosphere. In an age of increasing atmospheric carbon dioxide (CO_2), the large store of C in forest ecosystems has become increasingly important. Dixon et al. (1994) estimated the global C pool of forest ecosystems at 1150 Pg. These forested ecosystems include tropical, temperate and boreal forests. The boreal forest is of particular interest because of the large store of C in both the vegetation and the soil, which together account for 49% of the 1150 Pg of C (Dixon et al., 1994). The North American boreal forest stretches unbroken from eastern Canada westward across much of Canada to the central region of Alaska. It also covers extensive areas of Asia and Europe. Therefore, from a global perspective, the amount of C stored in the boreal forest is an important consideration when trying to understand and model the global C cycle.

Within the last 20 years, the introduction of eddy-covariance measurements over a variety of forest ecosystems has greatly improved scientists' understanding of the interaction between the forest and the atmosphere (Baldocchi et al., 1988). The eddy-covariance system measures the net uptake or loss of C continuously over a given area of forest, and can be expressed over hourly, daily and yearly time intervals. This

balance between C uptake through photosynthesis and C loss through respiration is referred to as net ecosystem productivity (NEP).

The eddy-covariance system operates year-round and can provide continuous estimates of NEP at time scales of minutes to years without disturbing the underlying vegetation. While eddy-covariance systems have provided a wealth of CO_2 flux data, few studies have provided an independent evaluation of these tower-based measurements of C uptake (Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002; Miller et al., 2004; Gough et al., 2007). In particular, there is a lack of studies in the boreal forest. One method of independent evaluation is the use of repeated biometric measurements of forest C stocks. These provide not only an estimate of the overall size of the stock but also the C stock change between sampling times, and show the component C stocks in which the changes are occurring. Biometric measurements of forest C stocks include the living vegetation, standing dead, woody debris, forest floor and mineral soil.

This project was part of the Boreal Ecosystem and Research Monitoring Sites (BERMS) study, the aim of which is to examine the role that the Canadian boreal forest plays in the global carbon, water, and energy cycles. BERMS is a major contributor to Fluxnet-Canada, a national research network studying C cycling in forest and peatland ecosystems across Canada. The study sites included a mature aspen (*Populus tremuloides* Michx.) stand and a mature jack pine (*Pinus banksiana* Lamb.) stand in Saskatchewan. The purposes of this study were to estimate the C stock change in these two forested ecosystems between 1994 and 2004, including changes in above- and below-ground biomass, standing dead, coarse woody debris, forest floor and mineral soil, and to compare this change with the 10-year cumulative NEP from eddy-

covariance. In addition to looking at the 10-year change, a second objective was to evaluate inter-annual differences in C uptake by comparing the annual stem C biomass increment with annual and growing season photosynthesis (GEP) and net C exchange (NEP), as measured by eddy-covariance.

Each experimental component is the focus of a stand-alone research paper, each with its own methodology, results and conclusions. The thesis is outlined as follows. A general literature review is provided in Chapter 2 to introduce relevant topics. Chapter 3 quantifies the total ecosystem C stocks and compares the 10-year stock change with 10-year NEP from eddy-covariance. Chapter 4 highlights the year-to-year changes in live stem biomass C uptake between 1994 and 2004 and compares it with annual estimates of GEP and NEP from eddy-covariance. General discussion and conclusions from Chapters 3 and 4 are provided in Chapter 5.

1.1 Literature Cited

Baldocchi, D.D., B.B. Hincks, and T.P. Meyers. 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69: 1331-1340.

Barford, C.C., S.C. Wofsy, M.L. Goulden, J.W. Munger, E.H. Pyle, S.P. Urbanski, L. Hutyra, S.R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294: 1688-1691.

Curtis, P.S., P.J. Hanson, P. Bolstad, C. Barford, J.C. Randolph, H.P. Schmid, and K.B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric. For. Meteorol. 113: 3-19.

Dixon, R.K., S. Brown, R.A Houghton, A.M. Solomon, M.C. Trexler and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263: 185-190.

Ehman, J.L., H.P. Schmid, C.S.B. Grimmond, J.C. Randolph, P.J. Hanson, C.A. Wayson, and F.D. Cropley. 2002. An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. Global Change Biol. 8: 575-589.

Gough, C.M., C.S. Vogel, H.P. Schmid, H-B. Su and P.S. Curtis. 2007. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. For. Meteorol. (in press).

Miller, S.D., M.L. Goulden, M.C. Menton, H.R. da Rocha, H.C. de Freitas, A.M.e Silva Figueira, and C.A.D. de Sousa. 2004. Biometric and micrometeorological measurements of tropical forest carbon balance. Ecol. Appl. 14: S114-S126.

2. LITERATURE REVIEW

2.1 Overview

The global carbon (C) cycle is one of the most studied topics in the natural sciences. The increasing concentration of carbon dioxide (CO_2) in the atmosphere since the industrial revolution is among the most significant of human influences on the global environment (Malhi et al., 1999), driving much of the research on the global C cycle. The global C cycle involves the cycling of C between the atmosphere, the oceans, and the vegetation and soils of the earth's terrestrial ecosystems. In particular, forest ecosystems comprise a major portion of the terrestrial C sink because of their large reservoirs of biomass and soil C (Table 2.1). Of these forest ecosystems, the boreal forest represents one of the largest pools of C on earth.

The boreal forest is a broad, circumpolar forest which covers over 14.7 million km^2, or 11% of the earth's terrestrial surface (Bonan and Shugart, 1989). The boreal forest is dominated by a variety of vegetation types, although species diversity remains low compared to other forest ecosystems, with only nine dominant tree species in North America (Landsberg and Gower, 1997). The current mosaic of vegetation across the landscape is a direct result of recurring disturbances. Fire is the most important natural disturbance (Landsberg and Gower, 1997). Fire frequency in the North American boreal forest ranges from 50 to 200 years (Bonan and Shugart, 1989). Human disturbances include harvesting of forest products; however, because of low stem wood production and extreme climate, the boreal forest is one of the least managed forest ecosystems in

Table 2.1 The estimated current area extent and carbon stocks of the major forest biomes (from Dixon et al., 1994).

Forest biome	Area (Mha)	C Density: Vegetation (Mg ha^{-1})	C Density: Soils (Mg ha^{-1})	C Pool: Vegetation (Pg)	C Pool: Soils (Pg)
Boreal	1372	64	343	88	471
Temperate	1038	57	96	59	100
Tropical	1755	121	123	212	216
Total	4165	Mean 86	Mean 189	359	787

the world (Landsberg and Gower, 1997). Nonetheless, large-scale harvesting in the southern extent of the Canadian boreal forest has become economically important, especially to northern communities.

At a national scale, fire is recognized as driving much of the boreal forest C balance (Dixon and Krankina, 1993) due to the direct loss of large amounts of C from the ecosystems and the impact on the forest age-class structure. However, at a local scale the forest C balance is determined by stand age and the interactions between the forest and the local climate. Studying these interactions to better understand what is driving C sequestration in these ecosystems has become the focus of several large-scale research projects. The Boreal Ecosystem-Atmosphere Study (BOREAS) was initiated as a large-scale international investigation focused on providing a better understanding of the exchanges of C, water and energy between the boreal forest and the lower atmosphere (Sellers et al., 1997). Since the BOREAS project, the scientific community has realized the importance of measuring the exchanges of C, water and energy on a continuous basis in an effort to understand the climatic and biophysical factors that control these processes. Today, several follow-on projects (Boreal Ecosystem Research and Monitoring Sites, BERMS; Fluxnet-Canada Research network, FCRN) have contributed to the understanding of the factors influencing C uptake in the boreal forest.

2.2 Net Primary Production and Ecosystem Carbon Storage

The C balance of a forest is the net result of CO_2 uptake through photosynthesis and CO_2 emission through respiration. The living vegetation takes in C through photosynthesis whereby the plants convert CO_2 to carbohydrates. The total amount of C taken in over a given time interval is referred to as gross primary productivity (GPP).

Some of that C accumulates as biomass over time while some C is respired (autotrophic respiration, Ra) for growth and maintenance of the trees' physiological processes (Waring and Schlesinger, 1985). Over any time interval, the net C uptake by the vegetation (the difference between GPP and Ra, Figure 2.1) is called net primary productivity (NPP):

$$NPP = GPP - Ra \quad \text{(Eq. 2.1)}$$

Net primary production is not readily estimated from GPP data because of the difficulty is quantifying Ra (Grace, 2005). However, Waring et al. (1998) suggests that across a wide range of forest ecosystems that NPP remains a constant fraction of GPP implying that the proportion of C lost through Ra remains constant across different forest types. Their results indicated that total NPP/GPP was conservative at 0.47± 0.04 SD (standard deviation). As a result of the difficulty in calculating Ra, NPP is more commonly calculated from the relationship:

$$NPP = \Delta B + D + H \quad \text{(Eq. 2.2)}$$

where ΔB is biomass increment, D is detritus production and H denotes loss of tissue mass due to herbivory (Landsberg and Gower, 1997). Allometric equations are used to estimate total biomass, whereas biomass increment is calculated as the difference over measurement periods (Gower et al., 2001). Biomass increment can be estimated from diameter growth over several years for all trees in a plot, or radial growth can be determined retrospectively by collecting radial increment cores from trees in a given plot (Landsberg and Gower, 1997). Detritus production represents biomass that was acquired during the time interval but was subsequently shed or otherwise lost by the plants during the interval (Clark et al., 2001). It includes coarse and fine litterfall and

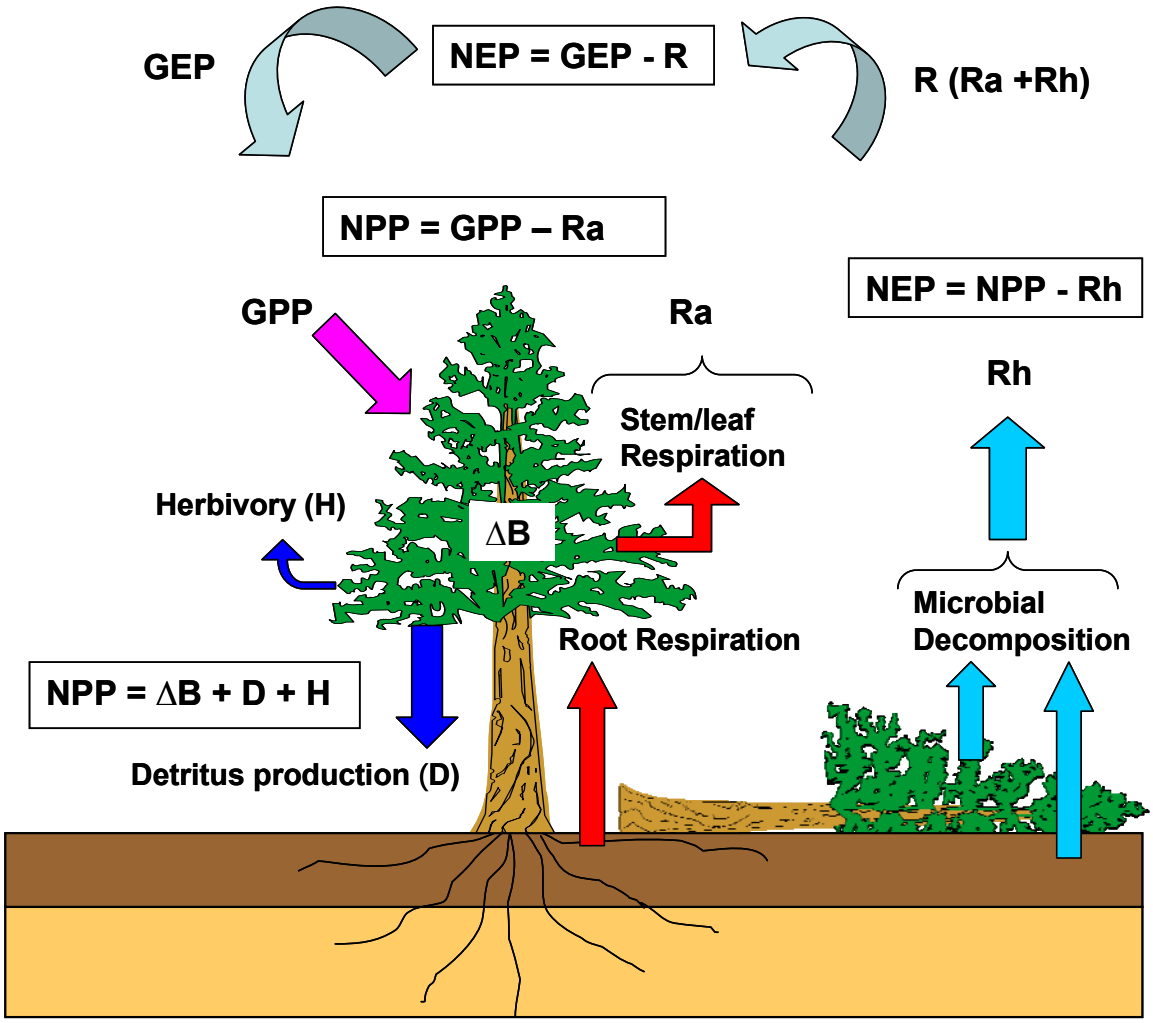

Figure 2.1 Conceptual diagram of the forest carbon cycle adapted from Gower et al. (2001). Abbreviations for fluxes are net ecosystem productivity (NEP), gross ecosystem photosynthesis (GEP), ecosystem respiration (R), net primary productivity (NPP), gross primary productivity (GPP), autotrophic respiration (Ra), heterotrophic respiration (Rh), biomass increment (ΔB).

fine root turnover. According to Gower et al. (1997), on average 56% of NPP for boreal forests becomes detritus. Herbivory is often ignored in forest production estimates because it is assumed to be a relatively minor factor (Landsberg and Gower, 1997), although aboveground production can be subject to substantial losses in some forest types, for example during insect outbreaks (Clark et al., 2001).

In addition to Ra C losses from forest ecosystems, the decomposition of organic material by microbial activity (heterotrophic respiration, Rh) evolves CO_2 to the atmosphere and further reduces the amount of C stored in the ecosystem. Therefore the net exchange of C (or net ecosystem productivity, NEP) in the whole ecosystem equals:

$$NEP = NPP - Rh \quad \text{(Eq. 2.3)}$$

Summarized in a different way, the overall balance between C uptake by photosynthesis (commonly referred to as gross ecosystem photosynthesis GEP, which is equal to GPP), and C losses from both *Ra* and *Rh*, equals NEP:

$$NEP = GEP - R \quad \text{(Eq. 2.4)}$$

where *R* is total ecosystem respiration, the sum of *Ra* and *Rh*. Net ecosystem productivity is positive when an ecosystem is gaining C from the atmosphere, indicating that the ecosystem in a C sink. Photosynthetic and respiratory fluxes are typically an order of magnitude greater than NEP, indicating that the net exchange of CO_2 is the difference of larger offsetting photosynthetic and respiratory fluxes (Baldocchi et al., 1997). Therefore, small changes in GEP or R may have a large impact on NEP, affecting the overall ecosystem C balance.

The overall forest C balance is affected by year-to-year changes in growing conditions and by longer-term climate shifts. Climate variability continually affects

forest ecosystems. Many large-scale research projects have tried to improve our understanding of the factors influencing C uptake in the boreal forest (BOREAS, BERMS, FCRN) and in other forest ecosystems around the world (AmeriFlux, Carbon EuroFlux, Oz Flux, Asia Flux, and the Large-Scale Biosphere Experiment in Amazonia (LBA)).

Eddy-covariance studies show significant inter-annual variability in NEP, resulting from the differential effects of climate variability on GEP and R (Barr et al., 2007; Kljun et al., 2006; Barr et al., 2004; Black et al., 2000). At the BERMS aspen site in the Canadian boreal forest, Black et al. (2000) found that earlier leaf emergence, the result of warmer springs, resulted in higher annual C sequestration. Indeed, the earlier the plants begin to photosynthesize, the greater the amount of potential CO_2 uptake by the forest. Additional studies of boreal ecosystems have highlighted the impact of drought (Kljun et al., 2006; Barr et al., 2007) and water table depth (Dunn et al., 2007) on the exchange of carbon. The study of inter-annual variability in C fluxes remains a priority for many long running eddy-covariance projects, particularly in light of predicted climate warming in the next two decades (IPCC, 2007).

2.3 Methods of Determining Forest Carbon Balances

At a stand level, there are several methods that can be used to determine an ecosystem's C balance including biometric techniques, chamber measurements, and micrometeorological methods, including eddy-covariance. One advantage of the eddy-covariance technique is that it operates year-round and can provide continuous estimates of NEP at time scales of minutes to years. Eddy-covariance is the only reliable method to measure NEP at time scales shorter than a few years. At these short time scales,

biometric approaches lack sufficient accuracy to characterize the time rate of change. One major disadvantage, however, is that eddy-covariance estimates do not provide details on where in the ecosystem the C is accumulating. Together both approaches provide independent assessments of ecosystem C storage.

2.3.1 Eddy-Covariance Technique

Eddy covariance measurements were first made about 40 years ago, but became more widely used in the late 1980s (Baldocchi et al., 1988). More recently, continuous CO_2 flux measurements have been made over a variety of ecosystems in an effort to evaluate the exchange of C between the vegetation and atmosphere (Barr et al., 2007; Dunn et al., 2007). At present, over 400 tower sites worldwide are operating on a long-term and continuous basis (FLUXNET, 2007).

The eddy-covariance method provides a direct measurement of the net exchange of CO_2, water vapour and sensible heat between a vegetated surface and the atmosphere (Baldocchi et al., 1988). The technique relies on atmospheric turbulence generated from the movement of air immediately above the earth's surface. Atmospheric turbulence causes the formation of eddies which transport heat and mass between the surface and free atmosphere. The basic principle of this technique is that the vertical flux of an entity in the turbulent surface layers is proportional to the covariance of the vertical eddy velocity and the entity's concentration (Fluxnet-Canada, 2007). Therefore, during periods of C uptake by the forest, CO_2-rich air moves down into the forest, while CO_2-poor air is correlated with upward vertical wind velocity. The covariance gives an estimate of the net amount of C absorbed or released by the forest, over a given area at

half-hourly timescales with minimal disturbance to the underlying vegetation, providing a reliable measure of NEP (Baldocchi et al., 1988).

Eddy-covariance measurements have provided valuable information about the interaction between the atmosphere and the terrestrial ecosystem since the early 1990s. Some highlights of boreal forest measurements include the long running, continuous measurements at the BERMS sites in Saskatchewan (Barr et al., 2007; Krishnan et al., 2006), the Northern Old Black Spruce site in Manitoba (Dunn et al., 2007) and several sites in northern Europe (Lindroth et al., 1998). Barr et al. (2007) reports a 9–year (1994,1996-2003) average NEP of 1.7 Mg C ha^{-1} yr^{-1} for the mature aspen BERMS site in Saskatchewan, with annual values ranging from 0.55 to 3.7 Mg C ha^{-1} yr^{-1}. Within a similar time period, Dunn et al. (2007) reports a 10-year (1995-2004) average NEP near zero for the Northern Old Black Spruce site in northern Manitoba. Over that time the ecosystem shifted from a C source in 1995 (-0.4 Mg C ha^{-1} yr^{-1}) to a sink in 2004 (0.2 Mg C ha^{-1} yr^{-1}).

2.3.2 Biometry

The ability to accurately and precisely measure the C stored and sequestered in forests is increasingly gaining global attention in recognition of the role forests have in the global C cycle (Brown, 2002). As discussed, the eddy-covariance technique provides an estimate of the net exchange of C above an ecosystem but actual sampling of the vegetation provides an independent verification of these tower-based estimates. Repeated biometric measurements of forest C stocks provide an estimate of the overall size of the stock as well as the C stock change between sampling times, and show which component stocks are changing. Biometric measurements of forest C stocks include the

living vegetation, standing dead, woody debris, forest floor and mineral soil. Established methods of measuring C in forests exist from many sources and are summarized by Brown (2002).

The living vegetation is one of the largest C stock components of the ecosystem. Estimating the change in living biomass relies heavily upon allometric relationships relating tree biomass with easily measured parameters such as tree diameter at breast height (DBH) (Ehman et al., 2002). Allometry is useful because it allows the total live biomass of a forest or stand to be estimated, without having to destructively sample the trees. The equations are generally specific to species and site (Gower et al., 1997), however, several regional-scale equations for a wide range of species are available (Lambert et al., 2005).

The advantage of biomass inventories over eddy-covariance techniques is that they are direct, fairly unambiguous, technologically simple and relatively low cost (Malhi et al., 1999). The main disadvantage is that they are almost invariably incomplete, particularly with respect to changes in below-ground carbon in both roots and soil organic matter, and may have high uncertainties due to high variability among samples (Malhi et al., 1999).

2.3.3 Convergence of Eddy-Covariance and Biometric Techniques

Several researchers have compared biometric and eddy-covariance estimates of the forest C balance (Barford et al., 2001; Ehman et al., 2002; Curtis et al., 2002; Miller et al., 2004; Gough et al., 2007). Concurrent biometric and meteorological measurements allow for independent assessments of ecosystem C storage (Gough et al., 2007).

Barford et al. (2001) and Miller et al. (2004) report good agreement between mean annual estimates from C stocks and eddy-covariance for a temperate and tropical forest, respectively, providing evidence that the two independent estimates of the C balance can be reconciled at some sites. According to Barford et al. (2001), biometric estimates should not be expected to reconcile with eddy-covariance measurements of NEP in a single year; indicating longer time scales are needed. Similarly, Gough et al. (2007) found poor agreement annually between eddy-covariance and biometric estimates but found good agreement over five years of study. Eddy-covariance time series are now just becoming long enough to support these longer-term studies.

Often due to the uncertainty in both estimates, the comparison cannot be an absolute validation of one methodology against the other, but serves as a cross-validation of both approaches (Ehman et al., 2002). Curtis et al. (2002) proposed that root and soil C dynamics have the greatest uncertainty and merit more research.

2.4 Forest Ecosystem Components

Although the overall C balance of an ecosystem at any given time provides important information about that ecosystem, it is also important to know where in the ecosystem the C is being stored and accumulating. The rate at which these forest ecosystems will accumulate C is dependent on many factors, including species composition, climate, and stand age (Gower et al., 1997).

In forest ecosystems, C is stored in multiple pools. These C pools are dynamic and they change in different ways, with C being added to each pool through a variety of natural and anthropogenic processes and leaving each pool at varying rates either to enter another pool or to be re-emitted into the atmosphere (von Mirbach, 2000). These fluxes

of C are a critical component of the ecosystem and its functioning. Figure 2.2 depicts the primary C pools and fluxes in forest ecosystems.

Carbon accrues in forests not only in live biomass, but also in above and below-ground dead organic matter pools, including standing dead wood, forest floor litter, coarse woody debris, and soil organic matter (Curtis et al., 2002; von Mirbach, 2000). Gower et al. (1997) reported that for a boreal aspen forest, 59% of the total ecosystem C content is in the living vegetation whereas the remaining 41% is found in the detritus and soil C pools. These results compare to those reported for a temperate hardwood forest (Barford et al., 2001) where 63% and 37% of the total ecosystem C content were found in the living vegetation and the detritus and soil C pools, respectively.

2.4.1 The Living Biomass

As communities of long-lived plants develop on land, a fraction of NPP is allocated to perennial woody tissues that accumulate as biomass through time (Schlesinger, 1991). Carbon is allocated to the component parts of trees, affecting their growth patterns and their capacity to compete with other plants (Landsberg and Gower, 1997). Carbon is stored in the living biomass in the stem, branches, foliage, roots and understory vegetation. In addition, C allocation patterns can affect NEP through the amount of detritus and fine roots produced.

The living vegetation actively takes in C through photosynthesis. Gower et al. (2001) reported that average total NPP for 24 boreal forest stands was 4.2 Mg C ha^{-1} yr^{-1} ranging from 0.5 to 8.7 Mg C ha^{-1} yr^{-1}. On average, NPP was 1.7 times greater for deciduous than evergreen coniferous stands (Gower et al., 2001). The deciduous-coniferous difference in NPP reflected a similar difference in the biomass C stocks

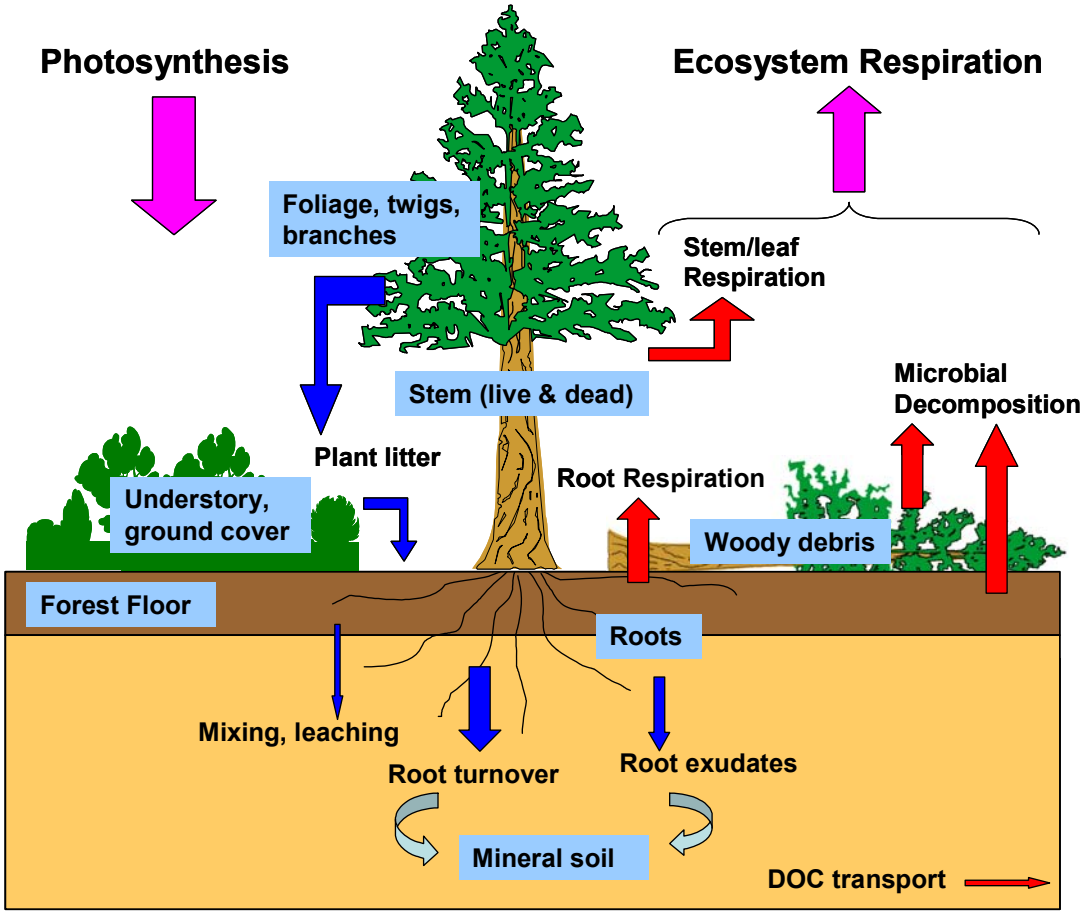

Figure 2.2 Forest ecosystem carbon stocks and fluxes. Stocks are represented by boxes and fluxes by arrows.

(Gower et al., 1997). In addition to differences in overall C uptake, Gower et al. (1997) found that coniferous species had greater allocation of C belowground compared to deciduous species. Gower et al. (2001) found that this greater allocation of C belowground in evergreen conifers was consistent across sites in North America, Northern Europe and Russia.

Currently, the allocation of C to roots and fine root turnover is not well understood because of a lack of empirical data, the result of the difficulty in making root measurements (Landsberg and Gower, 1997). Coarse root biomass can be estimated from allometric equations but the number of these equations is limited (Ruark and Bockheim, 1987; Bond-Lamberty et al., 2002) and their accuracy is uncertain. In terms of NPP, belowground components are often ignored or estimated as some theoretical proportion of aboveground values (Clark et al., 2001). In particular, fine root NPP remains a challenge to measure and quantify accurately. Although the overall size of the fine root pool at any given time is small, fine roots make a large contribution to total NPP due to their rapid growth and quick turnover rates (Kalyn and Van Rees, 2006). Despite these measurement challenges, the living vegetation and its productivity have a profound impact on the forest C balance.

2.4.2 Soil and Detritus

In boreal forest ecosystems, the soil is one of the largest C stocks with most of the C held in soil organic matter. Worldwide, 1550 Pg of C is found in soil organic matter (Schlesinger, 1991). The organic matter content of soil represents the integrated (net) balance between detrital inputs, both above- and below-ground, and organic matter losses from decomposition (Landsberg and Gower, 1997). Decomposition of dead

organic matter, plus root respiration, contributes to the soil CO_2 efflux. When detrital inputs exceed the C losses, C will accumulate in the soil. Schlesinger (1991) reports a mean accumulation rate for boreal forests of 8.7 g C m^{-2} yr^{-1} in the soil organic layer, known as the forest floor or LFH horizon.

The forest floor is one of the most dynamic components of forest ecosystems with annual inputs from aboveground litter and woody debris and outputs through decomposition. The dominant inputs of organic matter to the forest floor are aboveground (leaf, branch, stem, and reproductive structures) and below-ground (mycorrizhae and fine and coarse root turnover) detritus (Landsberg and Gower, 1997). Belowground detritus also represents a large input of C to the mineral soil. The mass of the forest floor C stock is also influenced by the age of the floor, or the elapsed time since the last fire or other disturbance (Fisher and Binkley, 2000).

The large amount of organic matter accumulation on the forest floor in the boreal region is a result of low temperatures, characteristic of that region, which limit decomposition (Van Cleve et al. 1991; Huang and Schoenau, 1996). The large forest floor C stock in the boreal region also results from the high C:N ratio of forest litter, which slows litter decomposition (Fisher and Binkley, 2000). The high C:N ratios are a consequence of the chronic nitrogen (N) deficiencies noted in the Canadian boreal forest (Weetman and Webber, 1972). Nutrients are released through the decomposition of litter inputs and subsequently mineralized and re-assimilated by plant roots. Nutrient availability not only affects the soil but has the potential to limit the forest's ability to take up C by limiting leaf area index (LAI) (Gower et al., 1997). Decomposition is therefore a critical ecological process in forest ecosystems. The forest floor provides

food and habitat for microflora and fauna, whose activity is essential to the maintenance of nutrient cycles in the soil.

In addition to the forest floor, the accumulation of dead wood on the soil surface, known as coarse woody debris (CWD), produces a major pool of detrital carbon. Tree mortality and falldown provide the primary input of C into the CWD pool. In an aging boreal aspen forest, yearly falldown rates for standing dead trees ranged from 9 to 20% (Lee, 1998). The subsequent decomposition of these dead trees is among the major controls of C retention in forest ecosystems (Yatskov et al. 2003). Harmon et al. (1986) provide an extensive review of the ecology of CWD.

The accumulation and decomposition of C in the CWD pool can directly affect the accumulation of C in the forest floor. The inputs of CWD vary over time and space (Yanai et al., 2003), leading to considerable spatial and temporal variability in forest floor C content. Both CWD and forest floor pools have high spatial variability. This increases both the difficulty in measuring temporal changes in C storage and the uncertainty in the resulting stock-change estimates. Several studies have suggested that resolving the uncertainty in the soil and detrital pools is an important issue deserving future work (Curtis et al., 2002; Barford et al., 2001).

Each ecosystem component contributes to the overall forest C balance through the addition, transfer and loss of C to and from each pool. The determination of the forest C balance is important locally, nationally and internationally, particularly in light of several international agreements focused on reducing the human impact on the global C cycle. In an age of increasing atmospheric CO_2 concentrations, the global C cycle and forest C research will continue to be at the forefront of scientific research.

2.5 Literature Cited

Baldocchi, D.D., C.A. Vogel and B. Hall. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. For. Meteorol. 83: 147-170.

Baldocchi, D.D., B.B. Hincks, and T.P. Meyers. 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69: 1331-1340.

Barford, C.C., S.C. Wofsy, M.L. Goulden, J.W. Munger, E.H. Pyle, S.P. Urbanski, L. Hutyra, S.R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO2 in a mid-latitude forest. Science 294: 1688-1691.

Barr, A.G., T.A. Black, E.H. Hogg, T.J. Griffis, A.D. Theede, N. Kljun, K. Morgenstern, and Z. Nesic. 2007. Climate controls on the carbon and water balances of a boreal aspen forest, 1994-2003. Global Change Biol. 13: 561-576.

Barr, A.G., T.A. Black, E.H. Hogg, N. Kljun, K. Morgenstern, and Z. Nesic. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. 126: 237-255.

Black, T.A., W.J. Chen, A.G. Barr, M.A. Arain, Z. Chen, Z. Nesic, E.H. Hogg, H.H. Nuemann, and P.C. Yang. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophys. Res. Lett. 27: 1271-1274.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological possesses in boreal forests. Annu. Rev. Ecol. Syst. 20: 1-28.

Bond-Lamberty, B., C. Wang, and S.T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. 32: 1441-1450.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges. Environ. Pollut. 116: 363-372.

Clark, D.A, S. Brown, D.W. Kicklighter, J.Q. Chambers, J.R. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: Concepts and field methods. Ecol. Applic. 11: 356-370

Curtis, P.S., P.J. Hanson, P. Bolstad, C. Barford, J.C. Randolph, H.P. Schmid, and K.B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric. For. Meteorol. 113: 3-19.

Dixon, R.K., S. Brown, R.A Houghton, A.M. Solomon, M.C. Trexler and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263: 185-190.

Dixon, R.K, and O.N. Krankina. 1993. Forest fires in Russia: carbon dioxide emissions to the atmosphere. Can. J. For. Res. 23: 700-705.

Dunn, A.L., C.C. Barford, S.C. Wofsy. 2007. A long-term record of carbon exchange in a boreal black spruce forest: means responses to interannual variability, and long-term trends. Global Change Biol. 13: 577-590.

Ehman, J.L., H.P. Schmid, C.S.B. Grimmond, J.C. Randolph, P.J. Hanson, C.A. Wayson, and F.D. Cropley. 2002. An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. Global Change Biol. 8: 575-589.

Fisher, R.F., and D. Binkley. 2000. Ecology and Management of Forest Soils. 3rd Edition. Wiley & Sons. Toronto.

FLUXNET, 2007. http://www-eosdis.ornl.gov/FLUXNET/. January 3, 2007.

Gough, C.M., C.S. Vogel, H.P. Schmid, H-B. Su and P.S. Curtis. 2007. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. For. Meteorol. (in press).

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele and T.K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102: 29,029-29,041.

Gower S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder and C. Wano. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl. 11: 1395-1411.

Grace, J. 2005. Role of forest biomes in the global carbon balance. p. 19-40. *In* H. Griffiths and P.J. Jarvis (ed.) The carbon balance of forest biomes. Taylor & Francis Group, New York.

Harmon,, M.E.,J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr. and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. in Ecol. Res. 15: 133-302.

Huang, W.Z. and J.J. Schoenau. 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorous and sulphur in a boreal aspen forest soil. Can. J. Soil Sci. 76: 373-385.

Intergovernmental Panel on Climate Change (IPPC). 2007. http://ipcc-wg1.ucar.edu/index.html. April 25, 2007.

Kalyn, A.L. and K.C.J. Van Rees. 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. 140: 236-243.

Kljun, N., T.A. Black, T.J. Griffis, A.G. Barr, D. Gaumont-Guay, K. Morgenstern, J.H. McCaughey, Z. Nesic.2006. Response of net ecosystem productivity of three boreal forest stands to drought. Ecosystems 9: 1128-1144.

Krishnan, P., T.A. Black, N.J. Grant, A.G. Barr, E.H. Hogg, R.S. Jassal, and K. Morgenstern. 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. Agric. For. Meteorol. 139: 208-223.

Lambert, M.-C., C.-H. Ung, and R. Raulier. 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. 35: 1996-2018.

Landsberg, J.J., and S.T. Gower. 1997. Applications of physiological ecology to forest management. Academic Press. Toronto.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecol. Manag. 105: 263-272.

Lindroth, A., A. Grelle and A.S. Moren. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. Global Change Biol. 4: 443-450.

Malhi, Y., D.D. Baldocchi, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22: 715-740.

Miller, S.D., M.L. Goulden, M.C. Menton, H.R. da Rocha, H.C. de Freitas, A.M.e Silva Figueira, and C.A.D. de Sousa. 2004. Biometric and micrometeorological measurements of tropical forest carbon balance. Ecol. Applic. 14: S114-S126.

Ruark, G.A. and J.G. Bockheim. 1987. Below-ground biomass of 10-, 20-, and 32-year old *Populus tremuloides* in Wisconsin. Pedobiologia 30: 207-217.

Schlesinger, W.H. 1991. Biogeochemistry: An analysis of global change. Academic Press, Toronto.

Sellers, P.J., Hall FG, Kelly R.D., Black A., Baldocchi D., Berry J., Ryan M., Ranson K.J., Crill P.M., Lettenmaier D.P., Margolis H., Cihlar J., Newcomer J., Fitzjarrald D., Jarvis P.G., Gower S.T., Halliwell D., Williams D., Goodison B., Wickland D.E., Guertin F.E. 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. J. Geophys. Res. 102: 28,731-28,769.

Van Cleeve, K., F.S. Chapin III, C.T. Dyrness, L.A. Viereck. 1991. Element cycling in taiga forests: state-factor control. BioScience 41: 78-88.

von Mirbach, M. 2000. Carbon budget accounting at the forest management unit level: an overview of issues and methods. ISBN0-662-29244-8. Canadian Model Forest Network.

Waring R.H. and W.H. Schlesinger. 1985. Forest Ecosystems: concepts and management. Academic Press. Toronto.

Waring, R.H., J.J. Landsberg and M. Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18: 129-134.

Weetman, G.F. and B. Webber. 1972. The influence of wood harvesting on the nutrient status of two spruce stands. Can. J. For. Res. 2: 351-369.

Yanai, R.D., S.V. Stehman, M.A. Arthur, C.E. Prescott, A.J. Friedland, T.G. Siccama, and D. Binkley. 2003. Detecting change in forest floor carbon. Soil Sci. Soc. Am. J. 67: 1583-1593.

Yatskov M., M.E. Harmon, and O.N. Krankina. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33: 1211-1226.

3. BIOMETRIC AND EDDY-COVARIANCE ESTIMATES OF TEN-YEAR CARBON UPTAKE OF TWO BOREAL FOREST STANDS

3.1 Introduction

The forest carbon (C) budget is the balance between C absorption by the forest through photosynthesis and C loss through respiration and decomposition. Carbon accumulates in forests over time. Since the boreal forest is a relatively slow growing ecosystem, it is important to look at the long-term C sequestration in these forests at decadal rather than annual time scales. Two independent approaches can be used to determine the change in C stocks over time: the eddy-covariance method and repeated biometric measurements.

The eddy-covariance method has become the standard method for the measurement of C uptake and release from a variety of forest types around the world (Barr et al., 2004; Falge et al., 2002; Baldocchi et al., 1997; Barford et al., 2001; Miller et al., 2004). Net ecosystem productivity (NEP), measured from eddy-covariance, is the balance between C uptake by the ecosystem through photosynthesis (gross ecosystem photosynthesis, GEP) and C loss to the atmosphere through respiration (ecosystem respiration, R). One advantage of the eddy-covariance technique is that it operates year-round and can provide continuous estimates of NEP at time scales of minutes to years. One major disadvantage, however, is that eddy-covariance estimates show only the net C exchange. They do not provide details on where in the ecosystem C content is increasing or decreasing.

Repeated biometric measurements of forest C stocks provide an estimate of the overall size of the stock as well as the C stock change between samplings, and show where those changes are occurring. Biometric measurements of forest C stocks include the living vegetation, standing dead, woody debris, forest floor and mineral soil. These measurements of biomass and detrital C and their changes with time provide a much-needed bound on the rates of C sequestration estimated by the eddy-covariance system. However, biometric estimates should not be expected to reconcile with eddy-covariance measurements of NEP in a single year (Barford et al., 2001), therefore longer temporal scales (ie. a decade) are needed. Eddy-covariance time series are now just becoming long enough to support these types of longer-term studies.

Since 1994, NEP measurements have been made almost continuously over several forest stands in Saskatchewan. In addition, in 1994 Gower et al. (1997) quantified the forest C stocks for those same stands, providing an opportunity to repeat biometric measurements at those sites and compare the stock changes to the 10-year cumulative NEP from eddy-covariance. This type of comparison is necessary because it provides an independent evaluation of tower-based measurements of C uptake. At present, similar validation studies are limited (Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002; Miller et al., 2004; Gough et al., 2007) and are non-existent for boreal forest sites in Canada.

This project is a part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) study, the aim of which is to examine the role that the Canadian boreal forest plays in the global carbon, water, and energy cycles. BERMS is a major contributor to Fluxnet-Canada, a national research network studying C cycling in forest and peatland ecosystems across Canada.

The objective of this project is to estimate the C stock change in two forested ecosystems in Saskatchewan between 1994 and 2004, including changes in above- and below-ground biomass, standing dead, coarse woody debris, forest floor and mineral soil, and compare this change with the 10-year cumulative NEP estimates from eddy-covariance.

3.2 Materials and Methods

3.2.1 Site Descriptions

This study was conducted at two of the BERMS sites within the Fluxnet-Canada Research Network (Figure 3.1). The sites are mature aspen and mature jack pine stands located in the Mid-Boreal Lowland Ecoregion in the Boreal Plain Ecozone near Prince Albert, Saskatchewan (Acton, et al., 1998). The boreal forest climate is characterized by short, warm, dry summers and long, cold winters. The mean annual precipitation and air temperature in the BERMS study area are 467 mm and 0.4 ºC, respectively, based on climate normals for the period 1971-2000 at Waskesiu Lake (Environment Canada, 2005).

The BERMS Old Aspen (OA) site (53.63° N, 106.2° W) is located near the southern edge of the boreal forest in Prince Albert National Park, Saskatchewan, Canada. The overstory vegetation is composed of an even-aged stand of aspen (*Populus tremuloides* Michx.), naturally established after a forest fire in 1919 and 85 years old in 2004 (24m in height). The understory is mainly hazelnut (*Corylus cornuta* Marsh.) with a few other shrubs. Topography in the area is relatively level, and the fetch is uniform to at least 3 km in each direction from the tower (as summarized by Chen et al., 1999). The soil is an Orthic Gray Luvisol (loam to clay loam texture) with a forest floor (LFH)

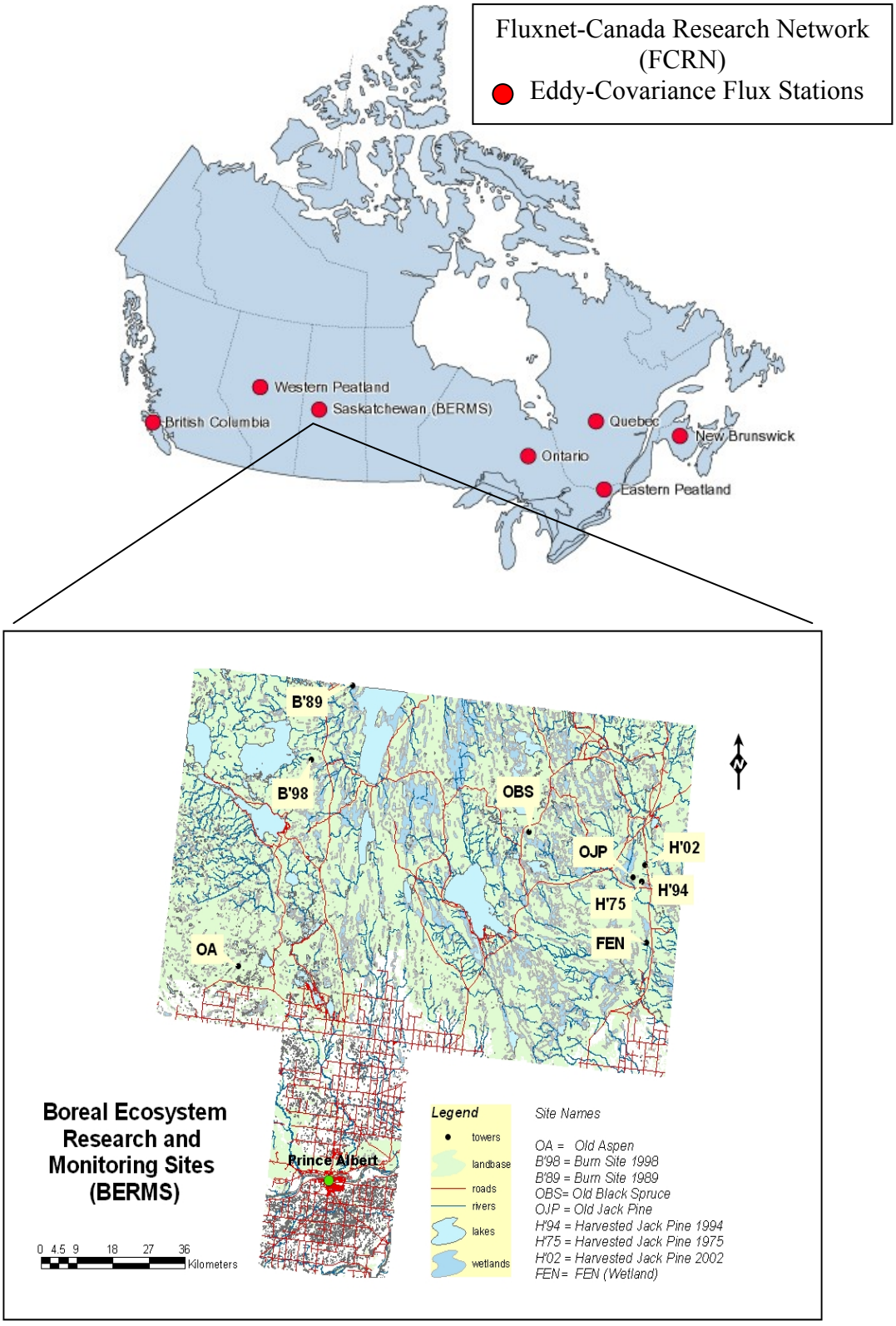

Figure 3.1 Map of the Boreal Ecosystem Research and Monitoring (BERMS) study area including Old Aspen (OA) and Old Jack Pine (OJP) (maps courtesy of Fluxnet-Canada, 2005 and Environment Canada, 2005).

8 to 10 cm deep.

The Old Jack Pine (OJP) site is located north east of Candle Lake, Saskatchewan. The overstory vegetation is composed of jack pine (*Pinus banksiana* Lamb.), with clumps of green alder (*Alnus crispa* (Ait.) Pursh) in the understory. The dominant ground cover includes some bearberry (*Arctostaphylos uva-ursi* (L.) Sprenge) and nearly continuous cover of reindeer lichen (*Cladina mitis* (Sandst.) Hale & Culb.). The soil is a coarse-textured, well drained sandy Brunisol.

In 1994, Gower et al. (1997) established four replicate plots (625 m^2) at each site immediately outside the footprint of the eddy-flux towers, in forest representative of that inside the footprint. At OA and OJP, three of the four plots were located and sampled in July 2004. Additionally, Fournier et al. (1997) established another larger plot (3000 m^2) immediately outside the flux footprint, which is used in this study for comparison with the Gower et al. (1997) plots. The large number of trees and the random locations of the plots are sufficient to adequately characterize the forest. Stand characteristics for each site are summarized in Table 3.1.

3.2.2 Above and Belowground Biomass

Total aboveground biomass of tree components (stem, branch, and foliage) was determined from allometric equations. A variety of allometric equations are available for the dominant overstory species (*Pinus banksiana* Lamb. at OJP and *Populus tremuloides* Michx. at OA). In August 1994, Gower et al. (1997) developed site specific allometric equations to convert stem diameter at breast height (DBH, 1.37m) into biomass estimates for each tree. However, the Gower et al. (1997) equations are based on a DBH range of 11.3-29.8 cm at OA and 6.6-18.8 cm at OJP and several trees now

Table 3.1 Selected stand characteristics at Old Aspen (OA) and Old Jack Pine (OJP) in July 2004.

Site	Stand Characteristics							
	Dominant Vegetation	Age	Trees†	Average DBH†	Basal Area†	Soil Sub-group‡	Forest Floor	Soil Texture
		years	ha^{-1}	cm	m^2ha^{-1}		cm	
OA	*Populus tremuloides* Michx.	85	656	24.1	30.7	Orthic Gray Luvisol	< 8	Loam to clay loam till
OJP	*Pinus banksiana* Lamb.	88	1024	14.9	18.8	Orthic Eutric Brunisol	< 5	Fine sand

† Calculated from trees in the Gower et al. (1997) plot

‡ Soil Classification Working Group (1998)

exceed this diameter range. As a result, these equations may no longer be appropriate. Extrapolating allometric equations beyond the diameter range has been shown to lead to large errors (Bond-Lamberty et al., 2002). Additionally, the Gower et al. (1997) equations are log-transformed equations. The transformation introduces a systematic bias into the calculations, and it has now become widely recognized that a correction factor is necessary to counteract this bias (Sprugel, 1983). Gower et al. (1997) applied a correction factor but it is unclear whether the correction factor follows the protocol of Sprugel (1983). Therefore the Gower et al. (1997) equations were not used in this study and 1994 values were re-calculated using the equation developed by Lambert et al. (2005).

Lambert et al. (2005) developed generalized biomass equations (non-log transformed) for the dominant tree species in Canada using both DBH-based and DBH- and height-based equations. The trembling aspen equations are based on a DBH range of 0.7-47.2 cm, whereas for jack pine it is 1.7-41.0 cm. These equations cover the range of DBH present in July 2004 at OA and OJP and are therefore more appropriate for use in this study.

Biomass for each tree within each plot was calculated using the DBH-based equation from Lambert et al. (2005). Each dominant overstory tree within the plots was permanently tagged in 1994; in July 2004, tree species, DBH, and description (live or dead) were tallied for each tree that was still standing. Standing dead C was estimated from the stem and branch allometric equations. Wood and foliage biomass were multiplied by 0.50 and 0.45, respectively, to estimate C content (Atjay, 1977; Matthews, 1993).

Total understory biomass was determined from dry biomass of all components in three 1m x 1m subplots randomly located in each of the replicate Gower plots. At the OA site, all vegetation in the plot was clipped and separated into annual herbs, woody tissue and new foliage. At OJP, where the understory consists of a few clumps of green alder and a nearly continuous ground cover of reindeer lichen, it was not feasible to separate the lichen from the forest floor. As a result, they were sampled together following the protocol developed by Howard et al. (2004). Samples were dried at 70ºC and weighed to the nearest 0.1 g.

Belowground biomass consists of both coarse and fine roots. At OA and OJP, coarse root biomass was determined from allometric equations developed by Ruark and Bockheim (1987) and Steele et al. (1997, unpublished data), respectively. These equations use DBH as the sole predictor of root biomass. Coarse root C content was assumed to be 50%. Fine roots are those roots that are considered < 2mm in diameter (Fisher and Binkley, 2000). Kalyn and Van Rees (2006) estimated fine root biomass from minirhizotron data, at both the OA and OJP sites in 2003 and 2004, using a plane intersect method developed by Bernier and Robitaille (2004). Organic C content of fine roots at OA and OJP was 46 % and 39 %, respectively (Kalyn and Van Rees, 2006).

3.2.3 Woody Debris

At the OA and OJP sites, woody debris transects were set up in both the Gower et al. (1997) and Fournier et al. (1997) plots in July 2004. Gower et al. (1997) and Fournier et al. (1997) did not measure woody debris in their studies, therefore data from Halliwell and Apps (1997) from OA and OJP was used to fill in this gap in the 1994 data.

Woody debris is defined as downed dead wood, which includes sound and rotting logs and uprooted stumps, usually described as dead, non-self-supporting woody material in various stages of decomposition that is located above the soil (NFI, 2002). Woody debris was measured using the line intersect method as described by Halliwell and Apps (1997) following the method developed by Van Wagner (1982) and McRae et al. (1979). The method involves setting out a line of known length, and tabulating the diameter of each debris item that intersects the line (Halliwell and Apps, 1997). The detrital volume (V) per hectare is calculated from:

$$V = \frac{\pi}{2L} \sum_{i=1}^{n} Ai \qquad \text{(Eq. 3.1)}$$

where L is the length of the sample line, and A_i is the cross-sectional area of the ith piece at the intersection. The final result was converted to cubic meters per hectare.

In the field, debris items were assigned to diameter classes (<0.5, 0.5-<1.0, 1.0-<3.0, 3.0-<5.0 and ≥5.0 cm) using a go-no-go-gauge with notches at 0.5, 1, 3 and 5 cm. For items ≥5.0 cm, diameter was measured using either a diameter caliper or a standard diameter tape. Items were identified by species, if possible, and visually assessed for the degree of decomposition (sound, sloughing, punky and rotten).

To calculate volume in diameter classes <5.0 cm using Equation 3.1, a mean diameter and specific gravity was assigned to each class (Halliwell and Apps, 1997). For items ≥5.0 cm, values of specific gravity were determined from the decomposition state. Halliwell and Apps (1997) assumed that rotten items have a specific gravity 0.10 less than sound items, while sloughing and punky items were assigned specific gravities interpolated at equal intervals (0.033) between sound and rotten values. Volume for

each diameter class was converted to detrital mass (Mg ha^{-1}) by multiplying volume and specific gravity. Woody debris was assumed to be 50% C.

3.2.4 Forest Floor and Mineral Soil

Forest floor and mineral soil samples were collected in each replicate plot at both sites. In 1994, Gower et al. (1997) collected soil samples in the replicate plots but only average values for each site were available for use in this study. As a result, the variability in the soil C change among plots between 1994 and 2004 cannot be directly resolved. The estimates of variability among plots assumed no variation in soil C.

At OA and OJP, three random locations were chosen to collect soil samples in each plot. Total soil C content was calculated for each horizon from horizon depth, bulk density, and percent carbon data. Four soil samples were collected from each horizon, averaged and summed to a depth of 70 cm below the ground surface. Percent total and organic C data was obtained through dry combustion of each sample (LECO Carbon Determinator CR-12 analyzer). Total soil C content was calculated by taking the C content of the soil profiles and averaging among the three replicate plots.

There were some sampling challenges at both sites when collecting forest floor samples. At OJP, it was not feasible to separate the lichen from the forest floor. Therefore, the forest floor samples contain the litter and humus layers as well as lichen, bryophytes and fine woody debris. Each sample was air dried with all live vegetation and live coarse roots removed, and ground to pass through a 0.2 mm sieve. A sub-sample was oven-dried at 110 ºC to a constant mass and weighed to the nearest 0.1 g. The total forest floor estimate was later divided back into its various components by assuming lichen, bryophytes and fine woody debris accounted for 41% of the forest

floor C content as reported by Vogel et al. (1998) for OJP in 1994. At OA, the clearest visual division between the forest floor and mineral soil occurred at the interface between the Ah and Ae horizons. In the field it was impossible to distinguish the organic horizons from the Ah horizons. Therefore, the C present in the Ah horizon was included in the estimate of forest floor C content.

3.2.5 Litter- and Tree-fall

Leaf and branch fall represent an important input of C to the forest floor. Litterfall data were provided by BERMS co-investigators. At OA, litterfall was collected in 1994 and from 1996 to 2005 (Ted Hogg, unpublished data), using methods described in Barr et al. (2004). At OJP, litterfall data have been collected every year since 2000 (Jagtar Bhatti, unpublished data).

At both sites, the aspen and jack pine overstory species have been dynamic over the last decade with many trees growing in DBH and height while other have died and/or fallen over. Tree mortality at both sites was determined by comparing the number of standing dead trees found in 1994 with that found in 2004. With the use of tagged trees within the replicate plots, each tree was labeled as live, standing dead or fallen. Fallen trees were identified as those that had a known tag in 1994 but were not found in the 2004 sampling. These trees became part of the CWD and forest floor pools.

3.2.6 Decomposition Rates

In order to understand the changes in detritus C stocks over time, the rate at which dead material is decomposing must be considered. Woody debris and fine litter decomposition rates were not measured in this study. However, extensive research has

been done on decomposition rates of northern species (Alban and Pastor, 1993; Laiho and Prescott, 2004; Sander, 2003; Trofymow et al., 2002). Decomposition of litter and coarse woody debris (CWD) is often modeled as an exponential decay process (Trofymow et al., 2002; Alban and Pastor, 1993). This function implies that the proportional rate of decay is constant over time and was initially used by Olson (1963). In this study, exponential decay rates were applied to the initial stock of CWD, the initial mass of the forest floor as well as the influx of C from falling trees and litterfall. The estimates of decay rates were not used directly in the C stock change calculations, which depended only on the C stock measurements. The decay rates were used as independent corroboration of the estimated detritus stock changes (Section 3.4.3).

The exponential rate of decay (k) for aspen wood of 0.025 yr^{-1} (Sander, 2003) used in this study is within the range proposed by Yatskov et al. (2003) for CWD of several species in Russia, and lower than those from Alban and Pastor (1993) for aspen in north central Minnesota. Sander (2003) reported that the decomposition rate of aspen wood in the western Canadian continental boreal forest is slower than the rates reported by Alban and Pastor (1993).

For the decomposition of jack pine wood, Sander (2003) reported a k of 0.014 yr^{-1} for Western Canada. Laiho and Prescott (2004) summarize a number of decomposition rates for northern coniferous species with values ranging from 0.0025 yr^{-1} to 0.071 yr^{-1} with a mean and median close to 0.020 yr^{-1}. Similarly, Yatskow et al. (2003) report a mean k for pine species in Russia of 0.020 yr^{-1}. Busse (1994) also reports an exponential rate of decay close to that of Laiho and Prescott (2004) and Yatskov et al. (2003) for Lodgepole pine in central Oregon (0.027 yr^{-1}). Alban and Pastor's (1993)

decomposition rate of 0.042 yr^{-1} is higher than the reported averages, likely because of increased moisture at their study sites compared to this study. Therefore, an average *k* of 0.020 yr^{-1} is used for jack pine wood.

At both sites, exponential decay rates for aspen and jack pine wood were applied to the estimates of CWD in 1994 from Halliwell and Apps (1997) to determine the amount of C remaining in 2004. Similarly, these decay rates were applied to new detritus that was added from treefall of both live and dead trees after 1994. In order to estimate falldown rates of the living trees and snags that became CWD, some assumptions were needed. First, it was assumed that the trees that died had grown at the same proportion as the other living trees, and second that 10% of the trees fell each year between 1994 and 2004. This study assumed that the detritus that fell in 1994-1995 decomposed for 9.5 years, while the 2003-2004 detritus decomposed for only 0.5 years.

Litterfall decomposition rates were applied to the initial forest floor C mass and the C input from litterfall between 1994 and 2004. Litterfall decomposition rates for aspen (0.097 yr^{-1}) and jack pine (0.095 yr^{-1}) (Trofymow et al., 2002), developed from sites near the present study area, were used at OA and OJP, respectively. Again it was assumed that the detritus that fell in 1994-1995 had been decomposing longer than the detritus that fell in 2003-2004.

3.2.7 Total Ecosystem Carbon Stocks and Ten-Year Change

Total ecosystem C stocks were calculated for each plot as the sum of each individual ecosystem component, and then averaged across plots for both 1994 and 2004 data. The total ecosystem C stock change was also calculated individually for each plot

and then averaged across the site. All values reported represent the mean and 95% confidence interval (CI).

3.2.8 Tower Flux Measurements

At OA and OJP, eddy-covariance measurements of carbon dioxide (CO_2), water vapour, and sensible heat flux densities were made at 39 and 29 m, respectively, above the ground from a twin scaffold tower (Griffis et al., 2003). All eddy-covariance data used in this study were collected and analyzed by BERMS investigators. At OA, flux measurements were made from February to September 1994 and then continuously since March 1996. At OJP, flux measurements began continuously in August 1999. Details of the eddy-covariance systems are given in Griffis et al. (2003), Black et al. (1996) and Chen et al. (1999).

The surface CO_2 flux, measured by eddy-covariance, provides a direct measurement of the net ecosystem exchange (NEE), the net exchange of CO_2 between the ecosystem and the atmosphere (Barr et al., 2004). If we neglect the loss of dissolved organic C via groundwater flow (Moore, 2003), NEE provides a direct measure of NEP (i.e., NEP = - NEE). Net ecosystem productivity results as the difference between C gains by gross ecosystem photosynthesis (GEP) and C losses by ecosystem respiration R, i.e., NEP = GEP - R. Note that NEP is positive for a C sink. The procedure to fill gaps in NEP and to estimate GEP and R is described in Barr et al. (2004). Net ecosystem productivity, GEP and R data provided for this study are in daily values (g C m^{-2} d^{-1}). At OA, the uncertainties in annual estimates of NEP were assessed by Krishnan et al. (2006) following Morgenstern et al. (2004). Systematic and random errors produced a maximum uncertainty in annual estimates of NEP of ± 0.4 Mg C ha^{-1}.

Similarly, Griffis et al. (2003) estimated the uncertainty in annual NEP as approximately ± 0.6 Mg C ha^{-1} and ± 0.2 Mg C ha^{-1} at OA and OJP, respectively, based on 2000 data.

At both sites, the time series (1994-2004) of NEP, GEP and R data is incomplete. At OA, flux data were not collected between October 1994 and March 1996, while at OJP flux data were not measured between 1995 and 1998. When eddy-covariance measurements were not available, *ecosys* modeled values were used. The *ecosys* model (Robert Grant, University of Alberta) was used to fill gaps in NEP, GEP and R data and to obtain an estimate of the total amount of C accumulated between 1994 and 2004 at both sites.

The *ecosys* model provides daily values of NEP, GEP and R for both sites. To validate the modeled values, we compared the model with measurements during the period of overlap. At OJP (2000-2004), the comparison showed that the *ecosys* model consistently underestimated R resulting in an overestimation of NEP. At OA (1996-2004), *ecosys* slightly overestimated NEP. In order to bring the model and eddy-covariance values in line with each other, a least-squares linear regression of modeled versus measured values was applied to daily NEP data to obtain adjusted model values that were used to fill in the missing periods.

3.3 Results

The change in ecosystem C content between 1994 and 2004 was measured through both biometric and micrometeorological techniques. At both OA and OJP, there was an increase in total ecosystem C measured by both techniques (Table 3.2). At OA, the change in total ecosystem C stocks between 1994 and 2004, using biometric techniques, was 18.2 ± 8.0 Mg C ha^{-1} (± 95% confidence interval, CI). At OJP, the

Table 3.2 Comparison of carbon budgets from biometric measurement of carbon stocks and eddy-covariance estimates of cumulative net ecosystem productivity (NEP) at Old Aspen (OA) and Old Jack Pine (OJP) between 1994 and 2004.

Comparison of C budgets	Old Aspen	Old Jack Pine
	Mg C ha^{-1}	
Biometric Δ C stocks	18.2 ± 8.0†	6.9 ± 1.6†
Eddy-covariance ∑ NEP	15.6 ± 4.0‡	5.8 ± 2.0§

† ± the 95% confidence interval

‡ ∑NEP ± uncertainty calculated from Krishnan et al. (2006)

§ ∑NEP ± uncertainty calculated from Griffis et al. (2003)

change in total ecosystem C stocks was 6.9 ± 1.6 Mg C ha^{-1}. Cumulative NEP from eddy-covariance and *ecosys* data, from 1 July 1994 to 30 June 2004 (Figure 3.2), was greater at OA than OJP with a net C uptake of 15.6 Mg C ha^{-1}, compared to 5.8 Mg C ha^{-1}, respectively (Table 3.2). See Barr et al. (2004, 2006) and Krishnan et al. (2006) for a detailed analysis of NEP, GEP and R at OA over this period.

3.3.1 Accounting of Individual Trees

Significant changes occurred in the distribution of C among the various ecosystem components. The number of living and standing dead trees decreased between 1994 and 2004 at both sites. The total number of trees tagged and measured for DBH in the Gower et al. (1997) plots at OA and OJP was 221 and 491 trees, respectively (Table 3.3). At OA in 1994, 175 of the 221 trees were living, and 46 were standing dead. In the same plots in 2004, 123 trees were living, 21 were standing dead, and 77 of the 221 had fallen to the ground. Similarly at OJP, in 1994 there were a total of 491 trees with 301 living and 190 standing dead. In 2004, the number of living trees dropped to 252, standing dead to 120, and the remaining 119 trees were on the ground. Similarly, there was a decrease in the number of trees living and standing dead in the Fournier plot (Table 3.3).

The Gower and Fournier plots had different tree mortality rates over the 1994-2004 period. In the Gower plots, tree mortality at OA and OJP was 29.7% and 16.3%, respectively. However, in the Fournier plot, tree mortality was slightly lower at OA (22.6%) and OJP (13.7 %).

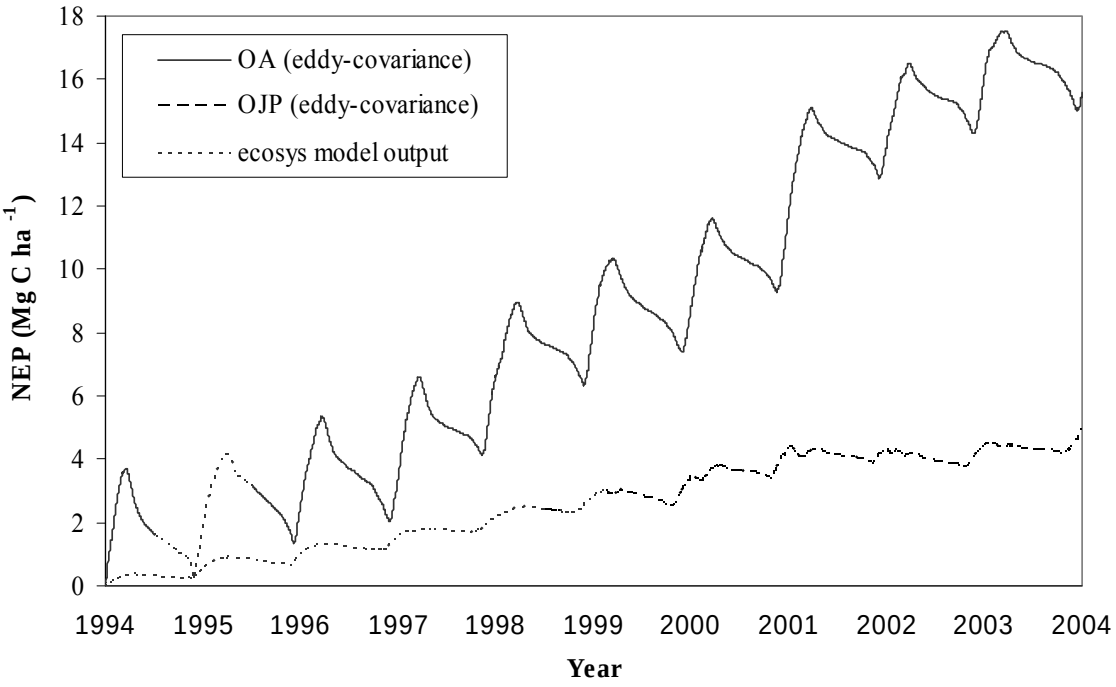

Figure 3.2 Cumulative daily net ecosystem productivity (NEP) (Mg C ha^{-1}) from eddy-covariance between 1 July 1994 and 30 June 2004 at Old Aspen (OA) and Old Jack Pine (OJP), supplemented by *ecosys* model data.

Table 3.3 Number of trees in each category (living, standing dead, and fallen) in the Gower and Fournier plots at Old Aspen (OA) and Old Jack Pine (OJP).

	Gower†		Fournier‡	
Site	1994	2004	1994	2004
	Number of Trees			
Old Aspen				
Living	175	123	296	229
Standing dead	46	21	60	39
Fallen		77		88
Total	221	221	356	356
Old Jack Pine				
Living	301	252	422	364
Standing dead	190	120	127	89
Fallen		119		96
Total	491	491	549	549

† total number of trees in three 25 m x 25 m plots set up by Gower et al. (1997)
‡ total number of trees in one 50 m x 60 m plot set up by Fournier et al. (1997)

3.3.2 Total Ecosystem Carbon

Total ecosystem C stocks were greater at OA in both years compared to OJP. In 2004, total ecosystem C stocks at OA were 180.6 ± 26.7 Mg C ha^{-1} (Table 3.4), more than twice the measured total of 78.9 ± 9.9 Mg C ha^{-1} at OJP (Table 3.5). At OA and OJP, the C in the living biomass was greater than total detritus at both sites in 1994, but at OA in 2004, the total detritus C was slightly higher than the biomass C. At both sites the amount of C stored in the living biomass ranged from 50% and 61% of the total ecosystem C content, with 36% to 41% in the stem component. In 2004, the stem component made the largest contribution to total ecosystem C ranging from 31.4 ± 6.2 Mg C ha^{-1} at OJP to 66.5 ± 16.6 Mg C ha^{-1} at OA. The mineral soil had the greatest store of detritus C at both sites in both years, accounting for 20% to 25% of the total ecosystem C content. Although both ecosystems increased in C content between 1994 and 2004, the distribution of C accumulation was different between the two sites (Figure 3.3).

3.3.3 Changes in the Living Biomass

At OJP, the largest increases in C storage occurred in the living biomass. At OJP, the change in live carbon storage between 1994 and 2004 was large (8.0 ± 0.6 Mg C ha^{-1}) compared to OA (2.0 ± 5.2 Mg C ha^{-1}) (Table 3.6). At OJP, live components increased from 40.1 to 48.0 Mg C ha^{-1} with increases in stem, branch and foliage components and only a negligible loss in the understory. The stem, branch and foliage components increased 5.0 ± 0.6 Mg C ha^{-1} between 1994 and 2004. When considering only the trees that survived the entire period, the living trees sequestered 10.2 ± 1.2 Mg

Table 3.4 Total ecosystem carbon distribution (Mg C ha^{-1}) by ecosystem component for a mature aspen stand (OA) in Saskatchewan.

	1994		2004	
Ecosystem Component	Mean	95% CI†	Mean	95% CI†
	Mg C ha^{-1}			
Living Vegetation				
Stem	67.0	± 18.1	66.5	± 16.6
Branch	8.4	± 2.3	7.6	± 2.0
Foliage	1.6	± 0.3	1.4	± 0.2
understory	0.7‡	n/a	3.3	± 1.5
Bryophyte/Lichen	---	---	---	---
coarse root	9.6	± 2.0	9.0	± 1.7
fine root	0.2§	n/a	1.7¶	n/a
Total overstory	77.0	± 20.7	75.5	± 18.8
Total live aboveground	77.7	± 20.7	78.8	± 20.1
Total live belowground	9.8	± 2.0	10.7	± 1.7
Total live	**87.5**	± **22.8**	**89.5**	± **21.8**
Detritus/mineral soil				
standing dead	8.6	± 1.8	6.1	± 1.8
coarse roots	1.3	± 0.3	0.8	± 0.2
coarse woody debris	9.7#	± 9.1#	13.8	± 3.6
forest floor	19.4‡	n/a	34.0	± 6.4
mineral soil	36.0‡	n/a	36.4	± 3.5
Total detritus	**75.0**	± **2.1**	**91.1**	± **4.9**
Total Ecosystem C	**162.5**	± **20.7**	**180.6**	± **26.7**

† 95% confidence interval (n=3)
‡ mean values only from Gower et al. (1997)
§ data from Steele et al. (1997)
¶ data from Kalyn and Van Rees (2006)
# data from Halliwell and Apps (1997), mean ± CI based on two plots (n=2)

Table 3.5 Total ecosystem carbon distribution (Mg C ha^{-1}) by ecosystem component for a mature jack pine stand (OJP) in Saskatchewan.

	1994		2004	
Ecosystem Component	Mean	95% CI†	Mean	95% CI†
	Mg C ha^{-1}			
Living Vegetation				
Stem	26.4	± 5.9	31.4	± 6.2
Branch	2.5	± 0.6	2.9	± 0.6
Foliage	1.8	± 0.3	2.0	± 0.3
understory	0.2‡	n/a	0.1	± 0.01
Bryophyte/Lichen	3.1§	n/a	3.4‡‡	± 0.7
coarse root	5.4	± 1.3	6.5	± 1.3
fine root	0.7¶	n/a	1.6††	n/a
Total overstory	30.7	± 6.7	36.4	± 7.1
Total live aboveground	34.0	± 7.7	39.9	± 7.9
Total live belowground	6.1	± 1.5	8.1	± 1.5
Total live	**40.1**	± **9.2**	**48.0**	± **9.4**
Detritus/mineral soil				
standing dead	6.6	± 2.2	5.3	± 2.1
coarse roots	1.2	± 0.4	1.0	± 0.4
coarse woody debris	1.6#	± 0.2#	3.6	± 0.2
forest floor	4.4§	n/a	4.8‡‡	± 0.8
mineral soil	18.2§	n/a	16.2	± 1.0
Total detritus	**32.0**	**± 1.8**	**30.9**	**± 3.2**
Total Ecosystem C	**72.0**	± **8.8**	**78.9**	± **9.9**

† 95% confidence interval (n=3)
‡ mean values only from Gower et al. (1997)
§ data from Vogel et al (1998)
¶ data from Steele et al. (1997)
# data from Halliwell and Apps (1997)), mean ± CI based on two plots (n=2)
†† data from Kalyn and Van Rees (2006)
‡‡ data from this study using proportion of lichen in forest floor from Vogel et al. (1998)

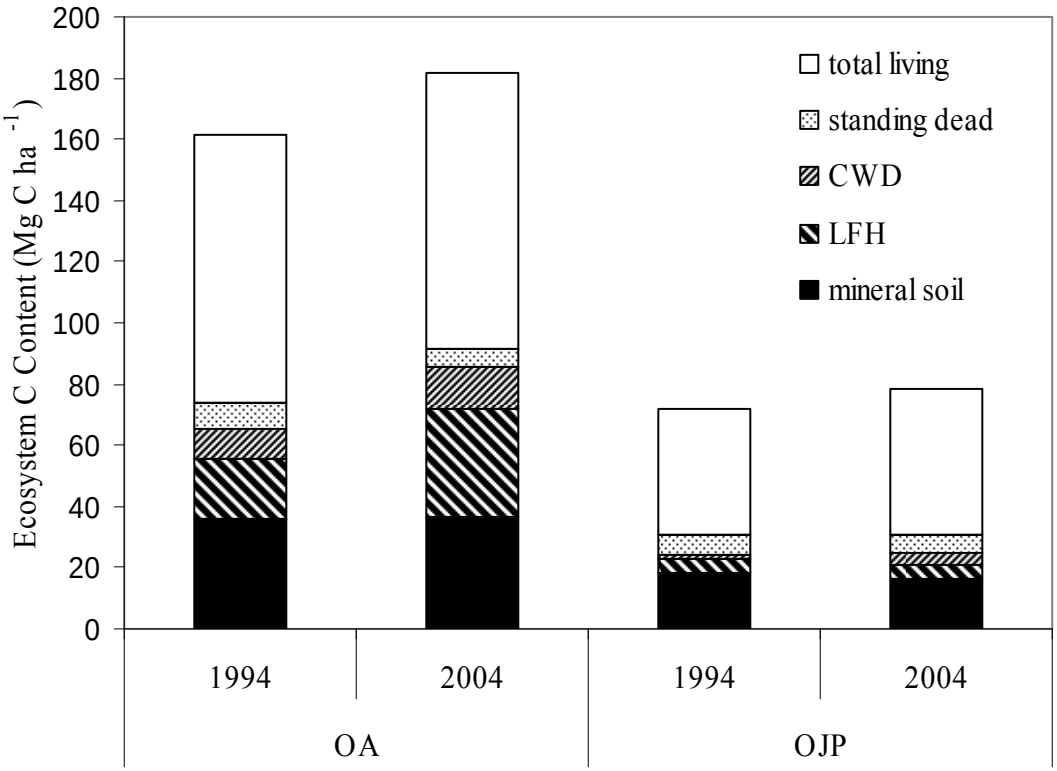

Figure 3.3 Total ecosystem carbon content and distribution at Old Aspen (OA) and Old Jack Pine (OJP) in 1994 and 2004.

Table 3.6 Ten-year carbon stock change by ecosystem component for a mature aspen (OA) and jack pine (OJP) stand in Saskatchewan.

	Old Aspen		Old Jack Pine	
Ecosystem Component	Mean change	95% CI†	Mean change	95% CI†
	Mg C ha^{-1}			
Living Vegetation				
Stem	-0.4	± 4.7	5.0	± 0.6
Branch	-0.8	± 0.7	0.5	± 0.1
Foliage	-0.2	± 0.1	0.2	± 0.0
understory	2.6	± 1.5	-0.1	± 0.0
Bryophyte/Lichen	0.0		0.3	± 0.7
coarse root	-0.6	± 0.7	1.1	± 0.1
fine root	1.5	n/a	1.0	n/a
Total overstory	-1.5	± 5.4	5.6	± 0.7
Total live aboveground	1.2	± 4.5	5.9	± 0.5
Total live belowground	0.9	± 0.7	2.1	± 0.2
Total live	**2.0**	± **5.2**	**8.0**	± **0.6**
Detritus/mineral soil				
standing dead	-2.5	± 3.3	-1.3	± 0.3
coarse roots	-0.4	± 0.4	-0.2	± 0.1
coarse woody debris	4.2	± 3.6	2.0	± 0.2
forest floor	14.6	n/a	0.4	± 1.0
mineral soil	0.4	n/a	-2.1	± 0.9
Total detritus	**16.2**	± **7.0**	**-1.1**	± **1.1**
Total Ecosystem C	**18.2**	± **8.0**	**6.9**	± **1.6**

C ha^{-1}. Between 1994 and 2004, C uptake by the jack pine stems made the largest contribution to the change in live components, contributing 72% to the total change in live C content between 1994 and 2004.

In contrast, at OA there was a decrease in C in all living vegetation between 1994 and 2004 except for in the understory vegetation (2.6 ± 1.5 Mg C ha^{-1}) and fine roots (1.5 Mg C ha^{-1}) (Table 3.6). The C change in the living aboveground aspen components (stem, branch and foliage) decreased -1.5 ± 5.4 Mg C ha^{-1} from 1994-2004. The results ranged from a net gain of C in plot 2 (4.0 Mg C ha^{-1}) to a net loss in plot 1 (-5.1 Mg C ha^{-1}) (Appendix D). Although the high tree mortality and treefall at OA caused the net change in aspen overstory C biomass to be slightly negative, the trees that were still alive in 2004 had grown substantially, taking up 18.1 ± 4.0 Mg C ha^{-1}. Moreover, there was no significant difference in the C uptake of living trees between the Gower and Fournier plots (t-test, t=-1.42, df=350, p=0.16) indicating a stable pattern of aspen growth across the site, with differences occurring in tree mortality and falldown rates.

Coarse and fine roots made a significant contribution to the total ecosystem C change, particularly at OJP. At OA, there was a decrease in live coarse roots of -0.6 ± 0.7 Mg C ha^{-1} while at OJP they increased by 1.1 ± 0.1 Mg C ha^{-1}. The change in fine root biomass C between 1994 and 2004 accounted for 14% and 8% of the total ecosystem C change at OA and OJP, respectively. However, the inconsistency in measurements of fine roots between the two samplings in 1994 and 2004 increases the uncertainty in this change at both OJP and OA. Therefore, these changes may not represent the true change in C in these pools over this period.

3.3.4 Changes in Detritus and Mineral Soil

At OA, the largest increases in C storage occurred in the detrital pools. The 10-year change in total detritus was 16.2 ± 7.0 Mg C ha^{-1} and -1.1 ± 1.1 Mg C ha^{-1} at OA and OJP, respectively. At OA, the forest floor saw the largest increase of 14.6 Mg C ha^{-1} which accounted for 90% of the total change in detritus and 80% of the total ecosystem C change (Table 3.6). The mineral soil was unchanged from 36.0 Mg C ha^{-1} to 36.4 Mg C ha^{-1}. In contrast, at OJP there was little to no change in the forest floor (0.4 ± 1.0 Mg C ha^{-1}) and a measured loss of C in the mineral soil (-2.0 ± 0.9 Mg C ha^{-1}). Both changes are well within the measurement uncertainty.

Coarse woody debris (CWD) increased from 9.7 Mg C ha^{-1} to 13.8 Mg C ha^{-1} at OA and from 1.6 Mg C ha^{-1} to 3.6 Mg C ha^{-1} at OJP. At OA in 2004, the CWD pool was the third largest detrital pool after the forest floor and mineral soil and accounted for 15% of the total detritus. Additionally, the relative contribution of each decomposition class to the total for items >5.0 cm was: sound (6.5%), sloughing and punky (54.8%) and rotten (38.7%). This distribution of decay classes changed by less than 8% in each class between 1994 and 2004. This comparison was not possible at OJP due to a lack of data from Halliwell and Apps (1997).

Standing dead trees and their associated dead coarse roots decreased at both OA and OJP between 1994 and 2004. At both sites, the change in C in dead coarse roots was negligible while the loss of C in standing dead trees was more substantial due to the decreasing number of standing dead trees during the period (Table 3.3).

3.4 Discussion

3.4.1 Total Ecosystem Carbon Stock Change and Net Ecosystem Productivity

It was hypothesized that the change in total ecosystem C stocks from biometric measurements would be equal to the change in C from the tower based eddy-covariance system. Several researchers have tried to compare biometric and eddy-covariance estimates of the forest C balance (Barford et al., 2001; Ehman et al., 2002; Curtis et al., 2002; Miller et al., 2004; Gough et al., 2007) and each of them acknowledge the difficulty in completing this type of analysis due to uncertainties in both estimates.

Ehman et al. (2002) found that annual biometric measurements, from an ecological inventory, were 14% and 31% higher than tower based measurements over a 2-year period, for a deciduous forest in Indiana. Miller et al. (2004) reported good agreement between annual biometric and micrometeorological estimates for a tropical forest in Brazil. Similarly, Barford et al. (2001) reported good agreement between mean annual estimates from C stocks and eddy-covariance for a temperate forest, providing evidence that the two independent estimates of the C balance can be reconciled at some sites. At the same site, Gough et al. (2007) reported poor agreement annually but good agreement over a 5-year period. The analysis by Gough et al. (2007) is one of the few studies comparing ecosystem C storage over several years. However, in general there appears to be an absence of comparisons of long-term C stock change and eddy-covariance over several years rather than annually.

In this study, the biometric measurements of the 10-year ecosystem C change were 17% and 19% greater than the tower based eddy-covariance measurements at OA and OJP, respectively (Table 3.2). Curtis et al. (2002) found no systematic pattern of

over- versus under-estimation of the biometric compared to the meteorological based measures for five sites in eastern North America. However, the general consistency between biometric and tower-base estimates in this study suggests that some confidence can be placed in both approaches, despite inherent, but not easily quantifiable uncertainties.

For the majority of the ecosystem components measured by biometry, the largest source of error is attributable to sampling (ie. inter-plot variability). For these components, the "range of potential estimates" was simply the 95% confidence intervals (Ehman et al., 2002) of the sampled data. Many of the ecosystem components exhibit high spatial variability increasing the uncertainty in some of the estimates. Particularly the root and soil C dynamics have been found to be large sources of uncertainty in biomass measures (Curtis et al., 2002) and more focused research is required in that area. Certainly the lack of detailed soil data from the 1994 sampling makes the analysis more difficult.

In addition to the uncertainty in the C stock changes, the lack of eddy-covariance data from 1995-1999 at OJP and uncertainty in the model makes any definitive conclusions about OJP difficult to make. However, it is evident that the tower-based approach at this site appears to be doing a good job characterizing the fluxes of C in and out of this forest. At both OA and OJP, the biometric and eddy-covariance measurements are consistent with each other, and taken in combination, provide strong evidence that the sites were C sinks during the study interval. This study is in agreement with Ehman et al. (2002) that the present comparison is not an absolute validation of one

methodology against the other, but may begin to serve as a cross-validation that gives insight into the strengths and weaknesses of both approaches.

Barr et al. (2007) reported a systematic -15% bias in eddy-covariance flux measurements of sensible and latent heat at these sites when compared with independent measurements of net radiation and surface storage (2000-2004). They also provided evidence that the negative bias may extend to the eddy-covariance measurement of NEP. The negative eddy-covariance bias is consistent with that reported in this study with regard to the measured C stock changes, although caution is warranted in using this study to justify energy-closure type adjustments to eddy-covariance measurements of NEP. The eddy-covariance versus biometric bias in this study is well within the measurement uncertainty of both techniques.

3.4.2 Ten-Year Change in Ecosystem Components

This study quantified the total ecosystem C content and its distribution among component C stocks for two boreal forest stands in 2004. The 10-year changes in component C stocks relied on previously published data for these two stands from 1994. However, the uncertainty in these changes remains a key issue in quantifying the total ecosystem C change. The uncertainty in the change of some components, such as fine root biomass C, coarse root biomass C and mineral soil C, exceeds the measurement uncertainty because of an inadequate sample size, a lack of detailed 1994 data or different sampling methodologies between years. At both sites, however, the 1994-2004 C stock change was dominated by a single component, the forest floor at OA and the living trees at OJP. For these stocks, the measured C stock changes significantly exceeded the measurement uncertainty, adding confidence that the estimated changes are

real. A summary of the 10-year change in ecosystem components is presented in Figure 3.4 (OA) and Figure 3.5 (OJP).

The measured C stock changes in the living trees at both OA and OJP have a high degree of credibility. The tree biomass C was calculated using the same allometric equations in both years based on the same set of trees. Furthermore, while the total ecosystem C content is sensitive to the allometric equation used, the change in these components is not. The total ecosystem C content and distribution presented in this study are consistent with other published data. In a concurrent study at OA, Ted Hogg (personal communication) reported a C biomass for the total live tree components of 91.4 Mg C ha^{-1} measured in 2000, compared to 84.5 Mg C ha^{-1} measured in this study in 2004. Martin et al. (2005) reported a total ecosystem C content of 147 Mg C ha^{-1} for a 65-year old boreal mixedwood forest in northern Manitoba, representing a middle value between the pure stands of deciduous and coniferous species presented in this study. The total live components accounted for 40% of the total ecosystem C content, compared with 50% and 61% at OA and OJP, respectively. The greater detritus pool at the site in northern Manitoba may be a result of cooler temperatures and slower rates of decomposition than in the more southern sites of OA and OJP.

Roots are an important component of the living biomass and many studies do not adequately account for root biomass C. For example, Gower et al. (1997) did not include roots into their ecosystem C total. In this study, coarse root C biomass was estimated using allometric equations. Like its aboveground counterparts, there was a decrease at OA and increase at OJP in coarse roots C biomass between 1994 and 2004. In 2004, the coarse root C biomass accounted for 5.0% and 8.2% of total ecosystem C

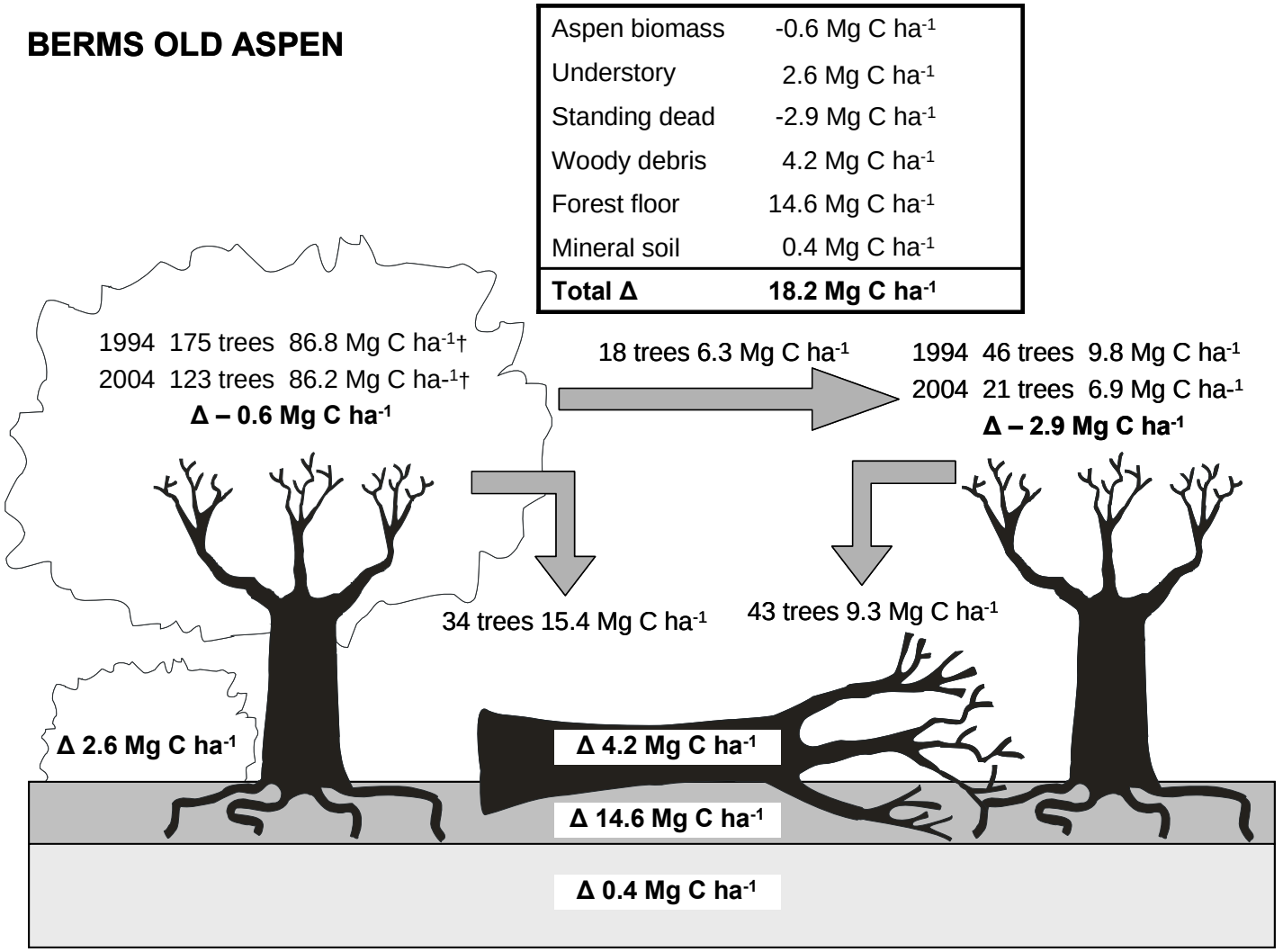

Figure 3.4 Change in carbon storage in each pool between 1994 and 2004 at Old Aspen (OA). † includes coarse and fine roots.

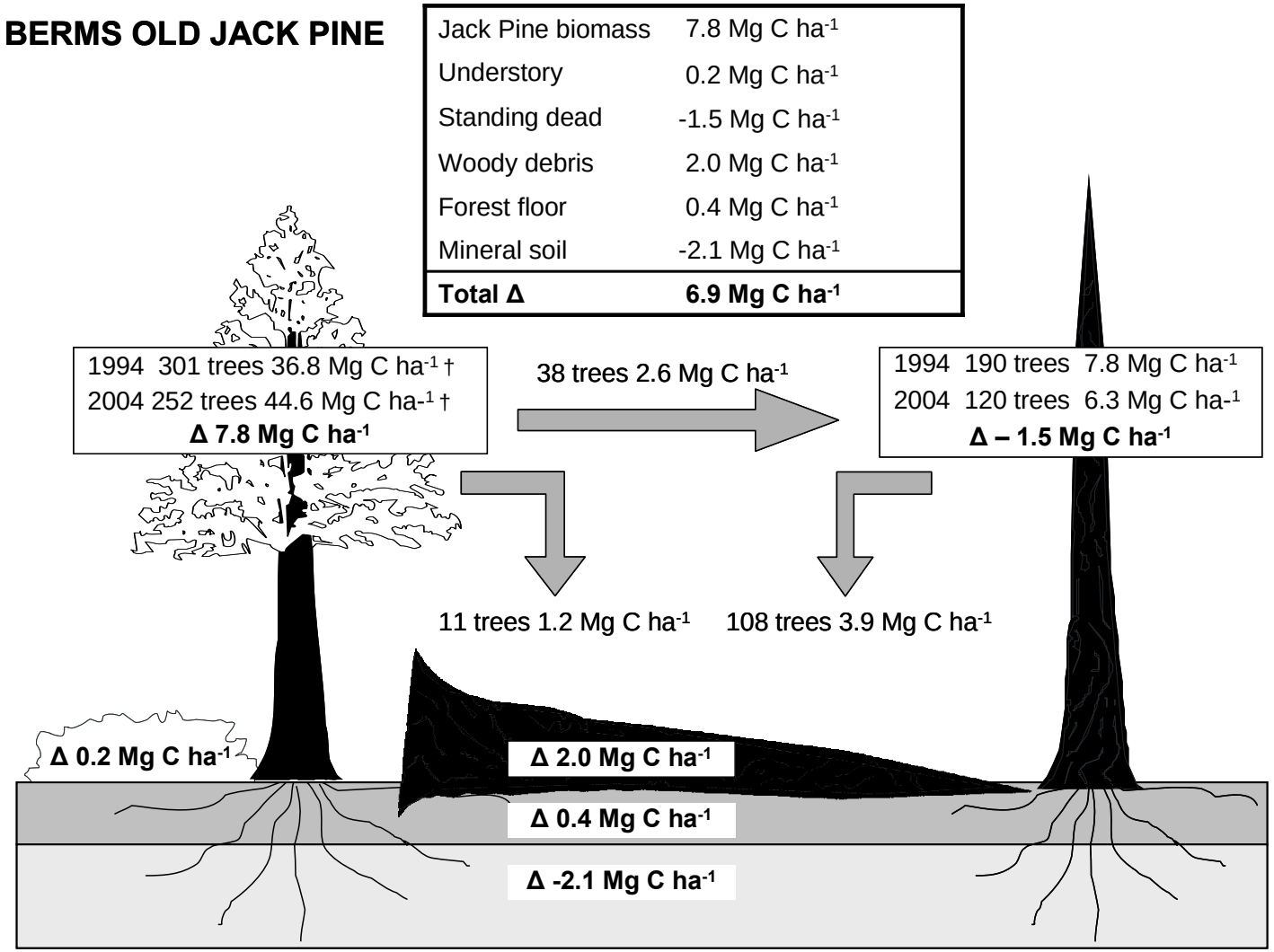

Figure 3.5 Change in carbon storage in each pool between 1994 and 2004 at Old Jack Pine (OJP). † includes coarse and fine roots.

at OA and OJP respectively. These values are similar to Martin et al. (2005), who found that coarse roots accounted for 6.7% of total ecosystem C for a boreal mixedwood forest. They are also similar to the earlier data of Steele et al. (1997) from OA and OJP, who reported coarse root biomass C values that are within 17% (OA) and 2% (OJP) of this study. However, Steele et al. (1997) reported much lower estimates of fine root biomass C in 1994 than Kalyn and Van Rees (2006) reported for 2004. Although the two studies utilized the same minirhizotron tubes at OA and OJP, different methodologies were used to determine fine root C biomass. This difference in methodology and the understanding that fine roots have a high turnover rate and therefore at any one time cannot store large amounts of C (Ruess et al., 2005), increases the uncertainty in the net change in fine root biomass C reported in this study. If Steele et al. (1997) underestimated fine root C biomass in 1994 the net change of C in this pool may be overestimated.

While the living components have undergone changes over the 10-year period so too have the detrital pools. The CWD pool represents an important store of detritus C. The rate at which it decomposes is among the major controls of C retention in forest ecosystems (Yatskov et al., 2003). At OA in 2004, values of CWD C content exceeded the range of estimates from Manies et al. (2005) for a black spruce chronosequence in northern Manitoba. Likewise, the estimates from Krankina et al. (2002) for forested regions of Russia are low relative to the results from OA, but similar to those at OJP, ranging from 2 to 7 Mg C ha^{-1}. In this study there is increased uncertainty in the C change in the CWD pools because the 1994 and 2004 CWD measurements were made in different plots. Because both Gower et al. (1997) and Fournier et al. (1997) did not

measure CWD in 1994, this study has used 1994 data from Halliwell and Apps (1997). Although the 2004 sampling methodologies followed those of Halliwell and Apps (1997), the high spatial variability in CWD inputs within these stands increases the importance of measuring these stocks changes within the same plots. In the summer of 2004, permanent markers were set up to facilitate re-measurement of the CWD stocks within the replicate plots and repeated sampling of this pool should be a focus of future research.

Like the CWD pool, the forest floor is one of the most dynamic components of forest ecosystems with annual inputs from aboveground litter and woody debris and outputs through decomposition. While litterfall inputs remain relatively steady from year to year, inputs of CWD vary over time and space (Yanai et al., 2003) and lead to large differences in forest floor C content. Therefore, detecting a change in C storage in the forest floor may be difficult over short time periods due to the challenges of adequately sampling the high spatial variability.

At OA, the largest change in ecosystem C stocks occurred in the forest floor pool. While many have measured forest floor C, few have reported changes in forest-floor C over a period of time. In 2004 at OA, the estimated forest floor C content from this study is within a range of values previously reported from a concurrent study at this site. Ted Hogg (personal communication) reported a range of 29.8 to 44.7 Mg C ha^{-1} with an average of 36.7 Mg C ha^{-1} during the summer of 2001. Other values from OA include an average forest floor C content of 46.9 Mg C ha^{-1} from Huang and Schoenau (1996) measured in 1994. However, the estimates from Ted Hogg and Huang and Schoenau (1996) were not measured within the same plots as this study. Because of the

high spatial variability in forest floor C (Yanai et al., 2003), measurement within the same plots is critical.

Unlike OA, at OJP there was a negligible change in forest floor C between 1994 and 2004. Nalder and Wein (1999) found no relationship between forest floor C and stand age for jack pine, which may explain the lack of change in the forest floor at OJP. At OJP, a range of forest floor C estimates from different studies include values of 2.7 Mg C ha^{-1} (Jagtar Bhatti, personal communication), 4.4 Mg C ha^{-1} (Vogel et al., 2000), 8.6 Mg C ha^{-1} (Howard et al., 2002), and 14.6 Mg C ha^{-1} (Gower et al., 1997). Each study used different sampling strategies and this makes comparisons difficult. However, the estimate of forest floor C from this study is well within the presented range of values. The wide range of forest floor C estimates at OJP reflects the high variability in ground cover at this site. The type of ground cover present can strongly influence the accumulation of organic matter directly underneath, particularly in jack pine forests. Nalder and Wein (1999) observed that forest floors under continuous lichen cover were invariably thin, while there were often substantial accumulations under continuous moss cover. At OJP, reindeer lichen covered 30% to 95% of the ground, while sphagnum moss only covered 2% to30%, and bare ground accounted for as much as 40% of the ground cover in some plots. This intermittent ground cover could have led to the large differences in forest floor C measurements at OJP.

At OA, the change in mineral soil C between 1994 and 2004 was negligible. This result is consistent with reports that mineral soil C is considered to be relatively stable in late-successional forests (Trettin et al., 1999). Unlike the forest floor, estimates of mineral soil C from other studies at OA and within Prince Albert National Park (Huang

and Schoenau, 1996; Fitzsimmons et al., 2004) are consistent with results from this study. At OJP, although there was a measured loss of C from the mineral soil pool, it may be an artifact of sampling design and not an actual loss of C from this pool. The mineral soil at OJP has been reported to be 92% sand (BOREAS data CD, unpublished data), and as a result retains little water and nutrients. It is likely neither gaining nor losing significant amounts of C.

As the site names suggest, both OA and OJP are relatively old forests approaching 90 years of age. Nevertheless, both forests are still accruing C. A comparison of the current rate of C accrual with the total ecosystem C stocks for these ~90-year-old stands shows that the current rate of C accrual is surprisingly high. Between 1994 and 2004, the total C stock increased by about 10% at both sites. Given that the initial C stocks were not zero, the implication is that annual NEP from 1994 to 2004 at these sites exceeded its long-term (90-year) mean, despite the mature age of the stands.

3.4.3 Detrital Carbon Dynamics

This study attempted to measure the total ecosystem C stock change directly from repeated measurements of the component C stocks. The strength of this study is the relatively long time period between sampling, which made it possible to detect changes. The results show significant C accumulation, although the uncertainty in some of the component stock changes is high. More specifically, the large change in forest floor carbon measured at OA raises the question of whether this change is real or simply a consequence of inadequate sampling protocols. This question was addressed by comparing the measured change in CWD and forest floor C stocks at OA and OJP with

independent estimates from detritus inputs and decomposition rates. The change in CWD and forest floor C stocks was estimated as the difference of the integrated above-ground litter inputs (fine litter and tree fall) and the decomposition of detritus C between 1994 and 2004.

Unlike the fine litter fall C inputs which were measured annually, the tree fall C inputs were estimated based on the trees that left the living and standing dead pools between 1994 and 2004. Because tree growth, mortality and falldown were not measured annually, it was necessary to assume that 10% of the living and standing-dead trees that entered the CWD pool fell each year and that, prior to dying, the trees that died had grown at the same rate as the trees that survived. Lee (1998) reported a yearly snag falldown rate ranging from 9-20% for a mature aspen forest, therefore our value of 10% is not unrealistic.

The decomposition calculations included both the detritus C stocks that were already in place in 1994 and those that were added through fine litter and tree fall between 1994 and 2004. For the latter, the decomposition calculation was based on the number of years the detritus was in place. The calculation used typical exponential decay rates outlined in Section 3.2.6. Table 3.7 summarizes decay rates and estimated mass remaining in the CWD and forest floor pools at both OA and OJP.

At OA, the estimated stock change in the CWD and forest floor pools was 20.1 Mg C ha^{-1} and corroborates the measured change in these pools of 18.8 Mg C ha^{-1}. Tree mortality and falldown had a strong impact on the C distribution between the living and detritus C pools because of the significant transfer of C from the living to the detritus pool. The input from falling trees contributed as much as 24.6 Mg C ha^{-1} to the CWD

Table 3.7 Estimated decomposition rates (k) of the initial stocks of coarse woody debris (CWD) and forest floor carbon (FFC) and the input of new trees and litter fall, amount remaining after a 10-year period and the net change in the combined CWD and FFC pools.

	Old Aspen				Old Jack Pine			
Ecosystem Component	k	Initial	Amount remaining	Net Change	k	Initial	Amount remaining	Net Change
			Mg C ha^{-1}				Mg C ha^{-1}	
Output from initial CWD C stock	0.025†	9.7	7.5	-2.2	0.020‡	1.6	1.1	-0.5
Output from initial FFC stock	0.097§	19.4	7.4	-12.1	0.095§	4.4	1.7	-2.7
Input from litterfall	0.097§	19.4	12.6	12.6	0.095§	6.5	4.2	4.2
Input from treefall	0.025†	24.6	21.8	21.8	0.020‡	5.1	4.6	4.6
Total estimated stock change				20.1				5.2
Total observed stock change				18.8				2.4

† Sander (2003)
‡ Yatskow et al. (2003)
§ Trofymow et al. (2002)

and forest floor pools between 1994 and 2004. It is clear that a large amount of C from these fallen trees entered the forest floor C pool within the 10-year period (Table 3.7). Additionally, a visual assessment of the forest floor revealed the presence of decomposing woody material providing further evidence that the forest floor received a large input of woody detritus between 1994 and 2004.

At OJP the net increase in the combined CWD and forest floor C pools was 5.2 Mg C ha^{-1}. While this is roughly double the measured change of 2.4 Mg C ha^{-1}, it is well within the measurement uncertainty. The discrepancy may be the result of either underestimated rates of decomposition or uncertainty in the change in the CWD pool due to the change in CWD measurement plots between 1994 and 2004. Decomposition rates are known to be slow in these types of environments and it is not known why there is so little organic material on the forest floor.

3.5 Summary and Conclusions

The C balance of the boreal forest is important regionally and globally and can be difficult to quantify. This study estimated the total ecosystem C change between 1994 and 2004 in two boreal forest stands using biometric and micrometeorological approaches. In addition to comparing the overall 10-year change between the two approaches, this study identified where in the ecosystem the C has accumulated.

According to the biometric approach, both sites were sinks of C between 1994 and 2004, with the greatest increase in C stocks occurring in the forest floor at OA and in the living vegetation at OJP. At OA, the observed change in the forest floor was 14.6 Mg C ha^{-1}. While the living trees at OA actively sequestered C over the decade of interest, an equal amount of C was lost from this pool through the death and falldown of

many trees, resulting in the large increase of C in the detrital pools. Input from falling trees contributed as much as 24.6 Mg C ha^{-1} to the CWD and forest floor pools between 1994 and 2004. This large input of C to the CWD and forest floor pools give credibility to the large change found in the forest floor pool at OA. In contrast, the live biomass C stock at OJP was less influenced by tree mortality and therefore increased substantially with a mean change of 8.0 Mg C ha^{-1}. Because the same trees were sampled in both years, a greater degree of confidence can be placed on the biomass C stock changes than in the changes in the detrital pools, which had higher sampling uncertainty.

The eddy-covariance technique also showed both sites to be net C sinks between 1994 and 2004. At both sites, the biometric and eddy-covariance estimates of the C sink strength were comparable. Between 1994 and 2004 the net change in C storage at OA according to the eddy-covariance approach was 15.6 ± 4.0 Mg C ha^{-1}, whereas the change in C stocks was measured as 18.2 ± 8.0 Mg C ha^{-1}. At OJP, the net change in C storage from eddy-covariance was 5.8 ± 2.0 Mg C ha^{-1} in comparison to 6.9 ± 1.6 Mg C ha^{-1} from the biometric approach. Due to the uncertainty in both estimates, any clear validation of one approach using the other is difficult. At OA the largest increase in the C stock occurred in the pool with the greatest uncertainty. More detailed sampling or a longer measurement period would be needed to reduce the uncertainty in the biometric estimates of the C stock change and use the biometric estimates to validate the eddy-covariance technique. Ehman et al. (2002) considers the evaluation of error in the results from both methods as the single most important issue deserving future work. One particular problem affecting this project was the lack of suitable benchmark values to constrain individual carbon budget values. Eddy-covariance measurements continue

to be made at both site and an effort should be made to repeat biometric measurements at OA and OJP in order to further reduce any uncertainties in the total ecosystem C stocks.

3.6 Literature Cited

Acton, D.F., G.A. Padbury and C.T. Stushnoff. 1998. The ecoregions of Saskatchewan. Saskatchewan Environment and Resource Management. Canadian Plains Research Centre, University of Regina.

Alban, D.H. and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23: 1744-1749.

Atjay, G.L., P Ketner, and P. Duvigneaud. 1977. Terrestrial primary production and phytomass. p. 129-181. *In* B.E. Bolin, T. Degen, S. Kempe and P. Ketner (ed.) The global carbon cycle. John Wiley, New York.

Baldocchi, D.D., C.A. Vogel and B. Hall. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. For. Meteorol. 83: 147-170.

Barford, C.C., S.C. Wofsy, M.L. Goulden, J.W. Munger, E.H. Pyle, S.P. Urbanski, L. Hutyra, S.R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO2 in a mid-latitude forest. Science 294: 1688-1691.

Barr, A.G., T.A. Black, E.H. Hogg, N. Kljun, K. Morgenstern, and Z. Nesic. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. 126: 237-255.

Barr, A.G., T.A. Black, E.H. Hogg, T.J. Griffis, A.D. Theede, N. Kljun, K. Morgenstern, and Z. Nesic. 2007. Climate controls on the carbon and water balances of a boreal aspen forest, 1994-2003. Global Change Biol. 13: 561-576.

Bernier, P.Y. and G.R. Robitaille 2004. The plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265: 165-173.

Black, T.A., G. Den Hartog, H.H. Nuemann, P.D. Blanken, P.C. Yang, C Russell, Z Nesic. X Lee, S.G. Chen, R Staebler and M.D. Novak. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biol. 2: 219-229.

Bond-Lamberty, B., C. Wang, and S.T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. 32: 1441-1450.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of Central Oregon. Soil Sci. Soc. Am. J. 58: 221-227.

Chen, W.J., T.A. Black, P.C. Yang, A.G. Barr, H.H. Neumann, Z. Nesic, P.D. Blanken, M.D. Novak, J. Eley, R.J. Ketler and R. Cuenca. 1999. Effects of climate variability on the annual carbon sequestration by a boreal aspen forest. Global Change Biol. 5: 41-53.

Curtis, P.S., P.J. Hanson, P. Bolstad, C. Barford, J.C. Randolph, H.P. Schmid, and K.B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric. For. Meteorol. 113: 3-19.

Ehman, J.L., H.P. Schmid, C.S.B. Grimmond, J.C. Randolph, P.J. Hanson, C.A. Wayson, and F.D. Cropley. 2002. An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. Global Change Biol. 8: 575-589.

Environment Canada. 2005
http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html

Falge E., D. Baldocchi , J. Tenhunen , M. Aubinet, P. Bakwin, P. Berbigier, C. Bernhofer, G. Burba, R. Clement, K.J Davis, J.A. Elbers, A.H. Goldstein, A. Grelle, A. Granier, J. Guðmundsson, D. Hollinger, A. Kowalski, G. Katul, B. Law, Y. Malhi, T. Meyers, R. Monson, J.W. Munger, W. Oechel, U.K.T. Paw, K. Pilegaard, U. Rannik, R. Rebmann, A. Suyker, R. Valentini, K. Wilson and S. Wofsy. 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. For. Meteorol. 113: 53-74.

Fisher, R.F. and D. Binkley. 2000. Ecology and Management of Forest Soils. 3rd Edition. Wiley & Sons. Toronto.

Fitzsimmons, M.J., D.J. Pennock, and J. Thorpe. 2004. Effects of deforestation on ecosystem carbon densities in central Saskatchewan Canada. Forest Ecol. Manag. 188: 349-361.

Fluxnet-Canada. 2006
http://www.fluxnet-canada.ca/home.php?page=home&setLang=en

Fournier, R.A., P.M. Rich and L. Landry. 1997. Hierarchical characterization of canopy architecture for boreal forest. J. Geophys. Res. 102: 29,445-29,454.

Gough, C.M., C.S. Vogel, H.P. Schmid, H-B. Su and P.S. Curtis. 2007. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. For. Meteorol. (in press).

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele, and T.K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102: 29,029-29,041.

Griffis, T.J., T.A. Black, K. Morgenstern, A.G. Barr, Z. Nesic, G.B. Drewitt, D. Gaumont-Guay, and J.H. McCaughey. 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. Agric. For. Meteorol. 117: 53-71.

Halliwell, D.H. and M.J. Apps. 1997. Boreal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: soils and detritus data. Northern Forestry Centre, Canadian Forestry Service.

Howard, E.A., S.T. Gower, J.A. Foley and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Global Change Biol. 10: 1-18.

Huang, W.Z., and J.J. Schoenau. 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorous and sulphur in a boreal aspen forest soil. Can. J. Soil Sci. 76: 373-385.

Kalyn, A.L. and K.C.J. Van Rees. 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. 140: 236-243.

Krankina O.L, M.E. Harmon, Y.A. Kukuev, R.F. Treyfeld, N.N. Kashpor, V.G. Kresnov, V.M. Skudin, N.A. Protasov, M. Yatskov, G. Spycher and E.D. Povarov. 2002. Coarse woody debris in forest regions of Russia. Can. J. For. Res. 32: 768-778.

Krishnan, P., T.A. Black, N.J. Grant, A.G. Barr, E.H. Hogg, R.S. Jassal, and K. Morgenstern. 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. Agric. For. Meteorol. 139: 208-223.

Laiho, R. and C.E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34: 763-777.

Lambert, M.-C., C.-H. Ung, and R. Raulier. 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. 35: 1996-2018.

Landsberg, J.J., and S.T. Gower. 1997. Applications of physiological ecology to forest management. Academic Press. Toronto.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecol. Manag. 105: 263-272.

Manies, K.L., J.W. Harden, B.P. Bond-Lamberty and K.P. O'Neill. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Can. J. For. Res. 35: 472-482.

Martin, J.L., S.T. Gower, J. Plaut and B. Holmes. 2005. Carbon pools in a boreal mixedwood logging chronosequence. Global Change Biol. 11: 1883-1894.

Matthews, G. 1993. The carbon content of trees. Forestry Commission, Technical Paper 4. Forestry Commission, Edinburgh.

McRae D.J., M.E. Alexander and B.J. Stocks. 1979. Measurement and description of fuels and fire behaviour on prescribed burns: a handbook. Canadian Forest Service, Great Lakes For. Res. Centre, Sault Ste. Marie, Ontario. Rep. O-X-287.

Miller, S.D., M.L. Goulden, M.C. Menton, H.R. da Rocha, H.C. de Freitas, A.M.e Silva Figueira, and C.A.D. de Sousa. 2004. Biometric and micrometeorological measurements of tropical forest carbon balance. Ecol. Applic. 14: S114-S126.

Moore, T.R. 2003. Dissolved organic carbon in a northern boreal landscape. Global Biogeochemical Cycles 17: 1109-1116.

Morgenstern, K., T.A. Black, E.R. Humphreys, T.J. Griffis, G.B. Drewitt, T. Cai, Z. Nesic, D.L. Spittlehouse and N.J. Livingston. 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. Agric. For. Meteorol. 123: 201-219.

Nalder, I.A., and R.W. Wein, 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochemical Cycles 13: 951-968.

NFI. 2002. National Forest Inventory: ground sampling guidelines. Working draft. Version 1.0. Canadian Forest Service.

Olson, J. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

Ruark, G.A. and J.G. Bockheim. 1987. Below-ground biomass of 10-, 20-, and 32-year old *populus tremuloides* in Wisconsin. Pedobiologia 30: 207-217.

Ruess, R.W., R.L Hendrick, J.G. Vogel, and B. Sveinbjornsson. 2005. The role of fine roots in the functioning of boreal forests. p. 189-210. *In* Chaplin, III, F.S. (Ed.) Alaska's Changing Boreal Forests. Oxford University Press, New York.

Sander, B. 2003. Post-fire structure and decomposition dynamics of coarse woody material in the western Canadian continental boreal forest. Ph.D. diss. University of Alberta, Edmonton.

Soil Classification Working Group. 1998. The Canadian System of Soil Classification. Agric. and Agric-Food Can. Publ. 1646 (Revised). 187pp.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209-210.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine, and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17: 577-587.

Trettin, C.C., D.W. Johnson, and D.E. Todd Jr. 1999. Forest nutrient and carbon pools at Walker Branch watershed: changes during a 21-year period. Soil Sci. Soc. Am. J. 63: 1436-1448.

Trofymow, J.A. T.R. Moore, B. Titus, C. Prescott, I. Morrison, M Siltanen, S. Smith, J. Fyles, R. Wein, C. Camire, L. Duschene, L. Kozak, M. Kranabetter, and S. Visser. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can. J. For. Res. 32: 789-804.

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Canadian Forest Service, Petawawa Natl. For. Inst. Chalk River, Ontario. Inf. Rep. PI-X-12.

Vogel, J., and S.T. Gower. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1: 386-400.

Yanai, R.D., S.V. Stehman, M.A. Arthur, C.E. Prescott, A.J. Friedland, T.G. Siccama, and D. Binkley. 2003. Detecting change in forest floor carbon. Soil Sci. Soc. Am. J. 67: 1583-1593.

Yatskov M., M.E. Harmon, and O.N. Krankina. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33: 1211-1226.

4. INTER-ANNUAL VARIABILITY IN LIVE STEM BIOMASS AND EDDY-COVARIANCE NEP AND GEP BETWEEN 1994 AND 2004 IN TWO BOREAL FOREST STANDS

4.1 Introduction

In any forest ecosystem the living biomass is a critical link in the carbon (C) cycle. Photosynthesis provides the main flux of C from the atmosphere to the biota. Carbon is lost from the ecosystem to the atmosphere through plant and microbial respiration. However, the uptake of C through photosynthesis and the loss of C through respiration can be quite variable from year-to-year. Annual growing-season conditions and potentially longer-term climate trends will affect year-to-year changes in C uptake and storage. Much research has concentrated on the inter-annual variability in the C balance within the Boreal Ecosystem Research and Monitoring Sites (BERMS) (Barr et al., 2007; Barr et al., 2004; Krishnan et al., 2006; Arain et al., 2002; Black et al., 2000; Griffis et al., 2003) and in different ecosystems around the world (Goulden et al., 1996; Dunn et al., 2007). Chapter 3 reported good agreement between 10-year eddy-covariance and C stock change estimates from 1994 to 2004. This chapter addresses the related question: is it also true that the eddy-covariance system is capturing the inter-annual variability in forest biomass increment at Old Aspen (OA) and Old Jack Pine (OJP)?

The annual changes in live stem biomass C at OA and OJP were assessed using tree ring increments to reconstruct historical diameters and annual increments, which were then scaled to the stand through the use of allometric equations. The other

components of net primary productivity (NPP), including branch, foliage, coarse and fine roots, understory and detritus production, were measured in some but not all years. Between 1994 and 2004, at the BERMS OA and OJP sites, the live stem was the largest store of live C in both ecosystems (Chapter 3). The factors affecting the growth of aspen in Western Canada are reasonably well-known (Hogg et al., 2005), however, little research has been done to determine whether and how the year-to-year fluctuations in tree rings are related to year-to-year patterns of ecosystem carbon dioxide (CO_2) flux (Rocha et al., 2006). No studies were found that compared inter-annual variability in stem biomass C storage and eddy-covariance measurements of gross ecosystem photosynthesis (GEP) and net ecosystem productivity (NEP).

This study analyses inter-annual variability in the live stem biomass C increment from two contrasting boreal forest stands, OA and OJP, and compares the stem C increment with annual and growing season GEP and NEP as measured by eddy-covariance. The primary objective was to evaluate inter-annual differences in both variables with the hypothesis that annual live stem biomass C increment for aspen and jack pine between 1994 and 2004 will correlate with the eddy-covariance estimates of photosynthesis. A secondary objective was to estimate NPP and the NPP/GEP ratio from these sites based on these and other measurements made during the BOREAS and BERMS studies (1994 to 2004).

4.2 Materials and Methods

4.2.1 Site Descriptions

A complete description of the BERMS Old Aspen (OA) and Old Jack Pine (OJP) sites can be found in Section 3.2.1.

4.2.2 Tree Ring Analysis

Tree cores were collected from a sub-sample of trees within 10 m of the replicate plots. Sampled trees were considered equivalent to those in the plots. The sampling protocol stratified the living tree population from each plot into three classes based on stem diameter at 1.3-m height (i.e., diameter at breast height, DBH). The DBH classes (small, medium, large) were equally sized in terms of their contribution to the total stem cross-sectional area of all trees within each plot. Tree cores were collected from small, medium and large trees, representing each DBH class, producing a total of twelve cores per plot. Cores were dried at 50ºC for 48 hours and prepared for analysis by polishing with progressively finer grades of sandpaper. Dry tree ring widths were measured using an ocular micrometer mounted on a compound dissecting microscope (Leica MZ 6, Leica Microsystems, and Wild M8, Wild Leitz Canada Ltd.) at 25x magnification.

In order to compare tree ring widths among different size classes, annual DBH increments were calculated as a proportion of the 2004 DBH. An average proportional DBH increment was calculated for the cored trees for each year, plot and size class. Based on the average proportional growth of the cored trees, the fresh (or non-dried) DBH was reconstructed for each year (1993-2004) for the surviving trees within the replicate plots. Only trees that survived the entire period were assessed.

4.2.3 Live Stem Biomass Increment

Once DBH was calculated for each tree in each year, DBH-based allometric equations (Lambert et al., 2005) were applied to determine annual stem biomass. Allometric equations provided biomass estimates for the stem component of aspen and jack pine trees. Annual biomass increments (1994-2004) were calculated as the

difference in biomass estimates for successive years and averaged across the replicate plots. Biomass was converted to C by multiplying by a factor of 0.5 (Matthews, 1993).

4.2.4 Tower Flux Measurements

A summary of eddy-covariance measurements of NEP and GEP is given in Section 3.2.8. Although modeling data are available to fill in gaps in the flux time series (Chapter 3) only years with complete eddy-covariance flux measurements were used. Flux data are generally presented as an annual sum based on a January to December year. The growth of tree rings however, is concentrated in the early growing season and often complete by August 1 of each year. In addition, there is evidence that C assimilated late in the growing season is allocated to early season growth the following year (Gough et al., 2007). Therefore, comparisons for this study were made using 12-month periods from August 1 (previous year) to July 31 (current year).

Eight years of complete flux data (1 August 1997 to 31 July 2004) were available at OA. In order to look at the C assimilated in the active part of the growing season and its impact on tree ring development a shortened period, from April 1 to July 31, was also considered. At OA, 10 years of early growing season flux data were available with 1995 missing. At OJP, five years of flux data were available (1994 to 1999 missing) for both the annual and growing-season time periods. However, flux measurement began on 15 August 1999; therefore 15 days of *ecosys* model data (Section 3.2.8) were used to fill in this gap in the flux data time series.

4.3 Results

4.3.1 Old Aspen

Annual aspen stem C biomass increment, as calculated from tree ring widths, ranged from 0.9 to 1.9 Mg C ha^{-1} yr^{-1} with the smallest increment recorded in 2002 and the largest in 2001 (Table 4.1). The 11-year (1994-2004) average annual aspen stem C biomass increment was 1.3 Mg C ha^{-1} yr^{-1}. The 8-year average stem C biomass increment, over the period with flux measurements (1997-2004), did not differ from the 11–year average of 1.3 Mg C ha^{-1} yr^{-1}. The coefficient of variation (CV) was 23% over the 11-year record. Stem C biomass increment showed the greatest deviations around the mean in the last four years of the time series (Figure 4.1a) whereas the first seven years remained relatively stable with a CV of 9%.

Cumulative GEP for 12-month periods, from August 1 to July 31, had an 8-year (1997-2004) average of 12.3 Mg C ha^{-1} yr^{-1}. Over the seasonal period when most radial growth occurs (April to July), cumulative GEP had a 10-year average (1994, 1996-2004) of 7.8 Mg C ha^{-1} yr^{-1}. Annual NEP and growing season NEP had an average C flux of 1.6 Mg C ha^{-1} yr^{-1} and 2.2 Mg C ha^{-1} yr^{-1}, respectively. The average values of growing season GEP and NEP did not change when based on 8- or 10-years of measurements.

The deviations in stem C biomass and annual GEP above and below their respective 8-year means are plotted in Figure 4.1a. In 1994, the stem C increment was equal to the 1997-2004 average. From 1997 to 2001, the stem C increment and GEP were above average with the exception of 2000 where GEP was slightly below average. The largest stem C increment and highest values of annual GEP were recorded in 2001 at 1.9 Mg C ha^{-1} yr^{-1} and 14.3 Mg C ha^{-1} yr^{-1}, respectively. The following year stem C

Table 4.1 Annual aspen stem biomass carbon increment (Mg C ha^{-1}), as calculated from tree ring widths and eddy-covariance estimates of gross ecosystem photosynthesis (GEP) and net ecosystem productivity (NEP) at Old Aspen (OA) summarized annually (August –July of following year) and over part of the growing season (April to July).

		GEP		NEP	
Year	Stem biomass C increment	Aug-July	Apr-July	Aug-July	Apr-July
			Mg C ha^{-1}		
1993-1994	1.32 (1.03)		8.6		2.9
1994-1995	1.28 (0.73)				
1995-1996	1.31 (0.74)		7.2		1.6
1996-1997	1.46 (0.68)	13.6	8.6	1.3	2.2
1997-1998	1.50 (0.87)	13.9	9.2	2.4	3.0
1998-1999	1.61 (0.91)	13.0	8.2	2.1	2.5
1999-2000	1.54 (0.68)	12.2	7.8	0.7	2.1
2000-2001	1.85 (0.98)	14.3	9.5	3.2	3.6
2001-2002	0.86 (0.50)	10.3	5.8	1.6	1.4
2002-2003	0.98 (0.45)	12.0	7.4	1.9	1.9
2003-2004	0.95 (0.57)	9.0	5.9	-0.1	0.7

Values in parentheses represent mean ± standard deviation. Standard deviation represent the among-plot spatial variation (n= 3)

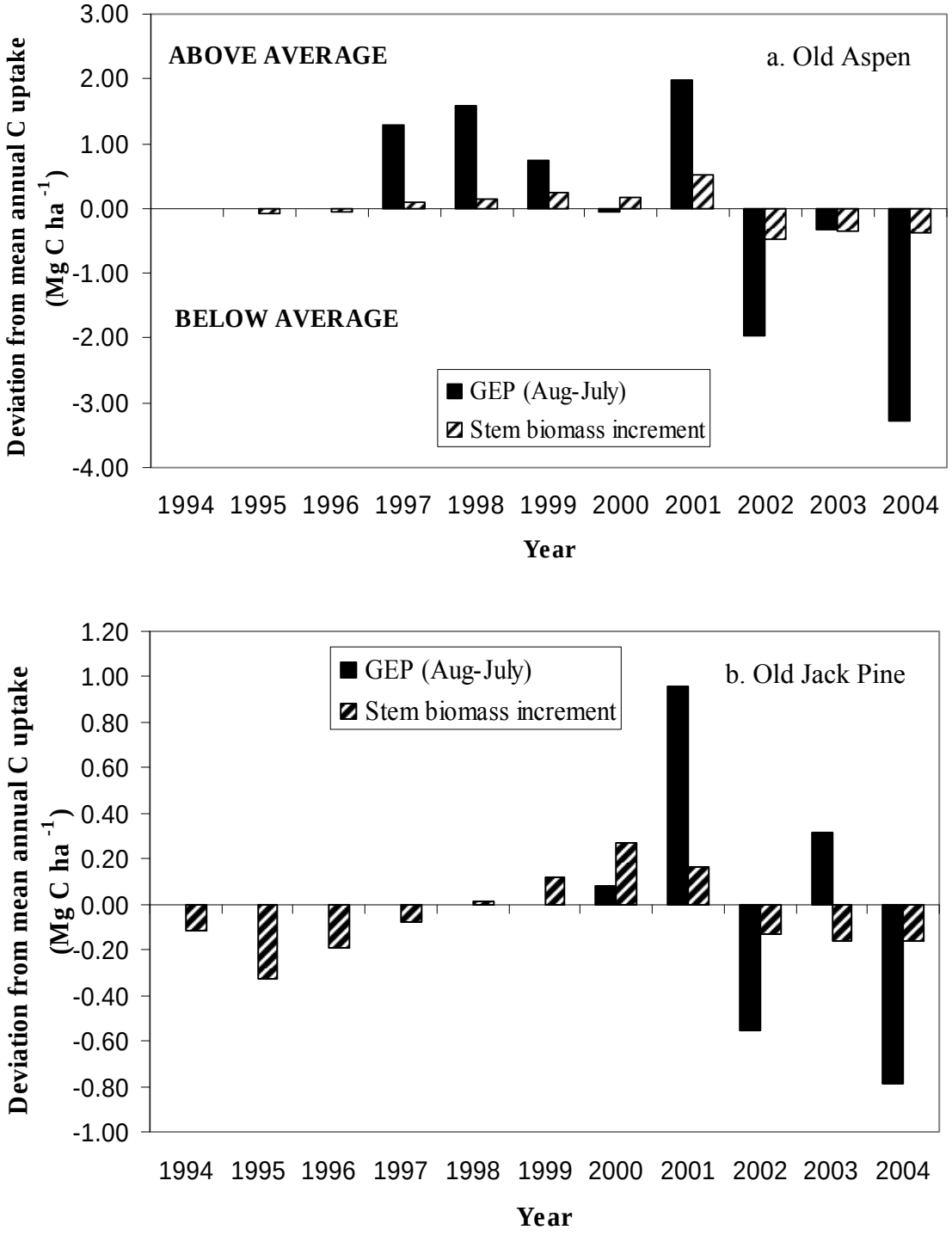

Figure 4.1 Deviation of annual carbon uptake from mean recorded values at **a.** Old Aspen (OA) and **b.** Old Jack Pine (OJP) based on annual eddy-covariance values of gross ecosystem photosynthesis (GEP) (August to July annually) and from tree ring estimates of stem biomass C increment for the period 1994 to 2004. (Note: at OJP stem biomass from 1994-2004 are presented but the average value is based on the five years with flux data).

increment hit an 11-year low of 0.9 Mg C ha^{-1} yr^{-1}, while GEP had the second lowest record of the time series. Both aspen stem C increment and GEP increased slightly in 2003 above 2002 values and then decreased in 2004. However, these three years (2002-2004) remain low relative to the rest of the time series.

Over the period of record, annual aspen stem C increment showed a better positive correlation with annual (August to July) GEP ($r^2 = 0.72$), than with annual NEP ($r^2 = 0.33$) (Figure 4.2a-d). The correlation improved when only the early growing season (April to July) was considered (Figure 4.2c), particularly in terms of cumulative NEP (Figure 4.2d). The most significant ($p = 0.001$) relationship was between stem C increment and growing season GEP in the April to July period (Figure 4.2c).

4.3.2 Old Jack Pine

Annual jack pine stem C increment ranged from 0.4 to 1.0 Mg C ha^{-1} yr^{-1} with the smallest increment recorded in 1995 and the largest in 2000 (Table 4.2). The 11-year (1994-2004) average annual jack pine stem biomass increment was 0.66 Mg C ha^{-1} yr^{-1}. For the period with flux measurements (2000-2004), the mean stem C increment was unchanged (0.7 Mg C $ha^{-1}yr^{-1}$). Annual GEP (August to July) averaged 7.0 Mg C ha^{-1} yr^{-1} over the 5-year record while cumulative growing season GEP averaged 4.1 Mg C ha^{-1} yr^{-1}. Annual NEP and growing season NEP had an average C flux of 0.38 Mg C ha^{-1} yr^{-1} and 0.62 Mg C ha^{-1} yr^{-1}, respectively (Table 4.2).

The 11–year record of stem C increment shows marked deviations above and below the 11-year mean (Figure 4.1b). From 1994 to 1997 stem increments were below average, whereas 1998 to 2001 were above average. The highest increments were recorded in 2000 and 2001, followed by three below average years (2002-2004). The

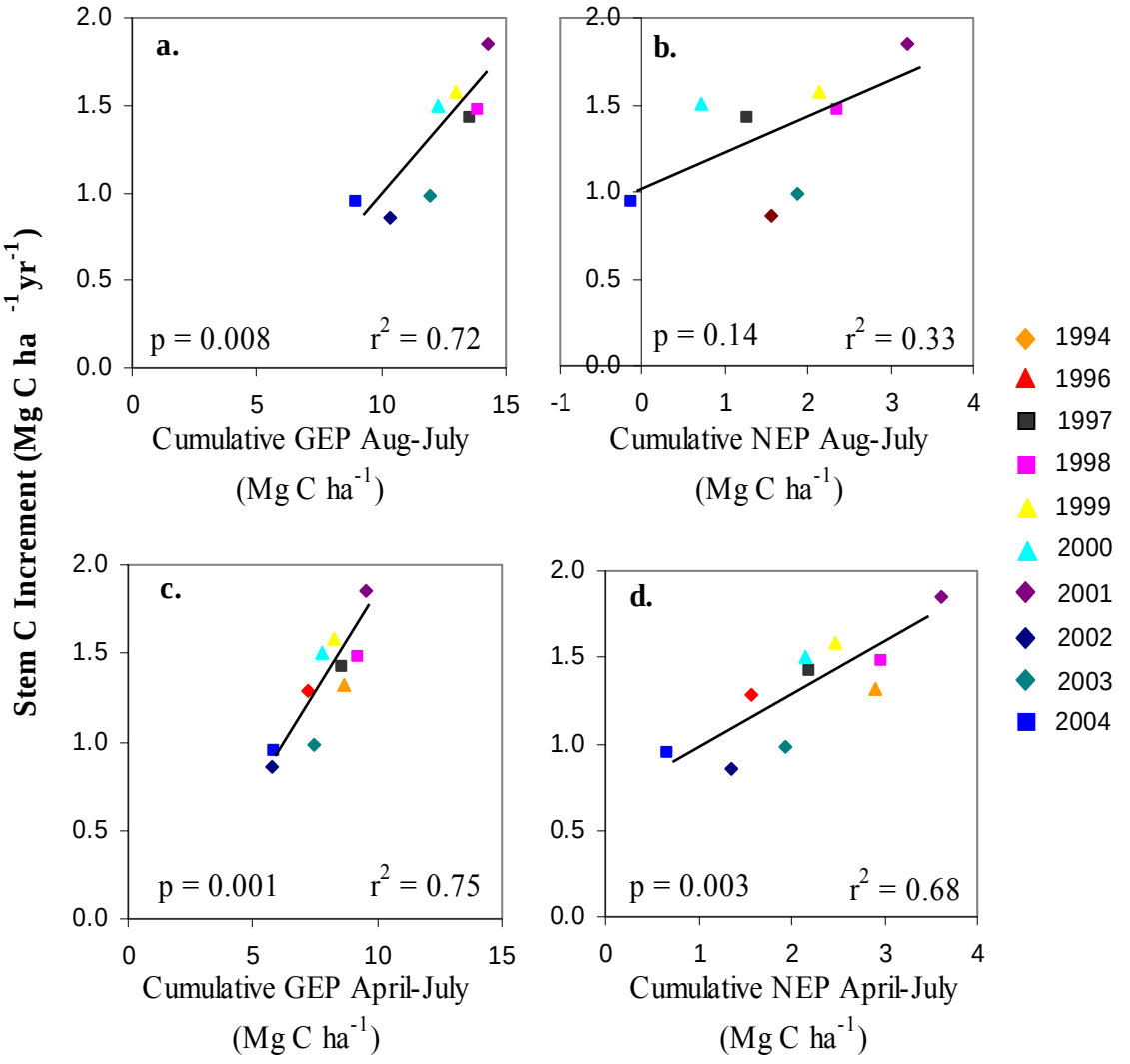

Figure 4.2 The relationship between annual stem carbon increment, as estimated from tree ring widths and eddy-covariance flux data at Old Aspen (OA). **a.** Annual gross ecosystem photosynthesis (GEP) (August 1 to July 31) equation of the line y = 0.1679x - 0.7059, **b.** Annual net ecosystem productivity (NEP) (August 1 to July 31) equation of the line y = 0.2012x + 1.0284, **c.** Growing season GEP (April 1st to July 31st) equation of the line y = 0.2132x - 0.320, **d.** Growing season NEP (April 1st to July 31st) equation of the line y = 0.304x + 0.6856.

Table 4.2 Annual jack pine stem biomass carbon increment (Mg C ha^{-1}), as calculated from tree ring widths and eddy-covariance estimates of gross ecosystem photosynthesis (GEP) and net ecosystem productivity (NEP) at Old Jack Pine (OJP) summarized annually (August-July of following year) and over part of the growing season (April to July).

		GEP		NEP	
Year	Stem biomass C increment	Aug-July	Apr-July	Aug-July	Apr-July
		Mg C ha^{-1}			
1993-1994	0.59 (0.11)				
1994-1995	0.38 (0.09)				
1995-1996	0.52 (0.12)				
1996-1997	0.63 (0.14)				
1997-1998	0.73 (0.18)				
1998-1999	0.83 (0.20)				
1999-2000	0.98 (0.23)	7.1	4.2	0.4	0.8
2000-2001	0.88 (0.19)	7.9	4.8	0.8	0.7
2001-2002	0.58 (0.09)	6.4	3.5	0.0	0.2
2002-2003	0.55 (0.10)	7.3	4.4	0.3	0.7
2003-2004	0.55 (0.11)	6.2	3.8	0.4	0.7

Values in parentheses represent mean ± standard deviation. Standard deviation represent the among-plot spatial variation (n = 3)

inter- annual variability in stem C increment at OJP is positively correlated to the inter-annual variability in stem C increment at OA between 1994 and 2004 (r^2=0.47, p=0.02) (Figure 4.3a). This relationship improves when only considering the first seven years of the time series (r^2 = 0.77, p = 0.008). Jack pine stem C increment shows greater variability (CV = 27%) than aspen stem C increment over the same period (CV = 23%). Particularly between 1994 and 2000, the jack pine stem C increment was more variable than the aspen stem C increment, reflected in its higher CV, 30% compared to 9%. On the other hand, in terms of GEP, OA exhibits greater variability (CV = 17%) than OJP (CV = 9%) between 2000 and 2004 (Figure 4.3b). Annual GEP at OA and OJP were positively correlated (r^2 = 0.96, p = 0.004), although the regression is limited to only five years of data. No significant relationship was found between NEP at the sites (not shown).

The deviations in jack pine stem C biomass and annual GEP above and below their respective 5-year means are plotted in Figure 4.1b. The deviations around the mean for stem biomass increment and GEP agree in four of five years. Jack pine stem C increment peaked in 2000, whereas GEP reached a maximum in 2001. Three years with stem C increments well below the mean were recorded between 2002 and 2004. The reduced growth is reflected in the GEP data of those years, except in 2003 where there is a large discrepancy between stem C increment and GEP. The large year-to-year changes in GEP observed between 2000 and 2004 make any pattern difficult to discern.

The regression analysis showed poor correlation between jack pine stem C increment and GEP and NEP flux data (Figure 4.4a-d). Including *ecosys* model output in the regression did not strengthen the relationships significantly (not shown). Over the 5-year record, jack pine stem C increment showed a slightly better positive correlation to

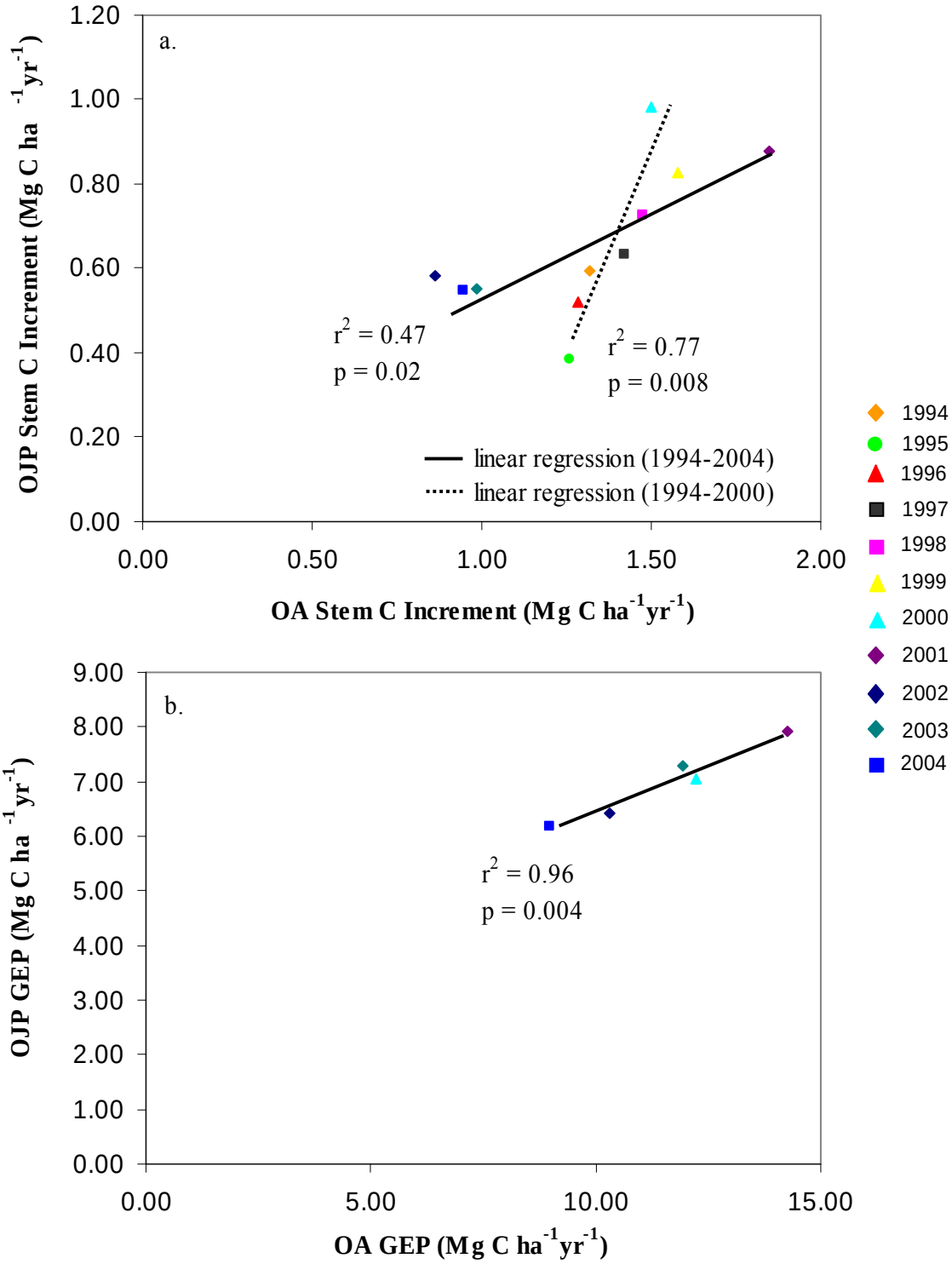

Figure 4.3 **a.** The relationship between annual stem carbon increment, as estimated from tree ring widths, at Old Aspen (OA) and Old Jack Pine (OJP) (equation of the solid line y = 0.4095x + 0.1179, dotted line y = 1.4484x - 1.3692), **b.** The relationship between annual cumulative GEP from eddy-covariance at OA and OJP (y = 0.34x + 3.0437).

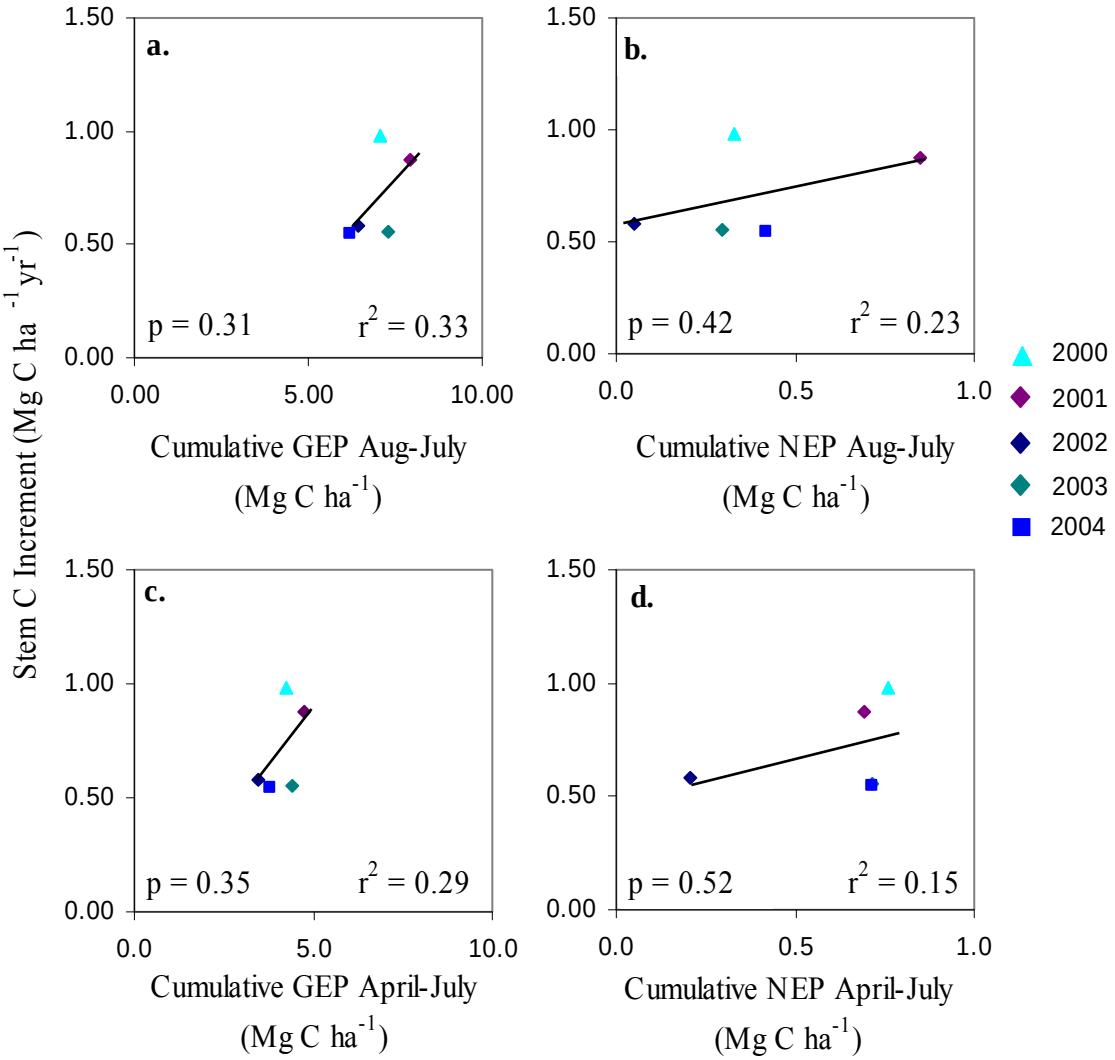

Figure 4.4 The relationship between annual stem carbon increment, as estimated from tree ring widths, and eddy-covariance flux data at Old Jack Pine (OJP). **a.** Annual gross ecosystem photosynthesis (GEP) (August 1st to July 31st) equation of the line y = 0.1716x - 0.488, **b.** Annual net ecosystem productivity (NEP) (August 1 to July 31) equation of the line y = 0.3372x + 0.5772, **c.** Growing season GEP (April 1 to July 31) equation of the line y = 0.2159x - 0.1828, **d.** Growing season NEP (April 1st to July 31st) equation of the line y = 0.3453x + 0.4948.

cumulative GEP (r^2 = 0.33) than to cumulative NEP (r^2 = 0.23) over the same periods, however, neither relationship was significant (Figure 4.4a,b). Additionally, the correlations of cumulative GEP and NEP did not improve when considering only part of the growing season (Figure 4.4c,d). The strongest correlation was between stem C increment and annual GEP, although not significant (p = 0.31) (Figure 4.4a). The regression analysis was clearly limited by the small sample size.

4.4 Discussion

4.4.1 Temporal Trends in Stem Biomass Carbon

This study compares a long-term record of eddy-covariance measurements of GEP with stem biomass C increment as determined from tree ring widths. Rocha et al. (2006) completed a recent study comparing whole forest gas exchange and tree ring width. Others have compared annual NEP budgets, of which stem biomass C is a component, with eddy-covariance measurements (Gough et al., 2007). In this study, tree ring widths were used to estimate the annual stem biomass C increment, and to determine the contribution of the stem C biomass to annual NPP.

Stem C increments in this study were similar to other studies at OA and OJP. At OA, the 5-year total stem C increment for 2000-2004 of 6.1 Mg C ha^{-1} was comparable to Hogg's unpublished data (Canadian Forest Service, CFS) for total stem C increment of 8.1 Mg C ha^{-1}, and well within his range from 3.8 to 10.6 Mg C ha^{-1}. At OJP, the annual tree ring width in mm calculated for this study, which forms the basis of the stem C increment results, are similar to the long-term average tree ring width (1980-2000) at OJP reported by Jagtar Bhatti (unpublished data, CFS).

Several factors influence the growth of trees as estimated by tree ring width. At OA, three consecutive years of drought (2001-2003) had a varying effect on stem C. In the first year of drought (2001), the stem C increment was above the 11-year average. Kljun et al. (2006) reported that in 2001 the reduction in the cumulative water balance had almost no effect on the soil water content at 30-60 cm. Consequently, stem growth does not appear to be affected in the first year of drought. As the drought continued into 2002 and 2003, the stem C increments were the lowest among the 11 years. Furthermore, stem growth continued to be suppressed in 2004 following the drought (Krishnan et al., 2006). These results are consistent with the conclusions of Hogg et al. (2005) that inter-annual variation in regional-scale aspen growth could be explained by two important factors: the climate moisture index (precipitation – potential evapotranspiration) and insect defoliation. The analysis of regional scale aspen growth in western Canada by Hogg et al. (2005) showed a tendency for aspen growth to recover in the year immediately following defoliation, whereas moisture deficits had a significant impact for up to four years. No incidents of insect defoliation were reported during the period of this study.

Like aspen, jack pine stem C increments were above the 11-year average in 2001 and then below average in 2002, 2003 and 2004. For a Scots Pine forest in Switzerland, the severe drought in the summer of 2003 resulted in a narrow tree ring for that year (Zweifel et al., 2006). Radial growth in the drought year was strongly influenced by current climatic conditions, namely the lack of precipitation during the growing season and high temperatures. Radial growth did not recover in 2004, despite normal precipitation. Zweifel et al. (2006) concluded that growth in 2004 in the Scots Pine

forest seemed to be influenced more by the previous year's precipitation rather than current conditions.

Stem C increment, at both OA and OJP, was adversely affected by drought in the latter part of the time series. Although, aspen stem growth appears to be more affected by this drought than jack pine (Figure 4.3a), the severity of the drought was not the same at both sites. Old Aspen received significantly less precipitation than OJP in 2001 and 2002 (Figure 4.5). Consequently, it would be premature to conclude that aspen growth is more sensitive to drought than jack pine. Nevertheless, between 1994 and 2004 the jack pine stem C increment showed greater inter-annual variability than aspen (Figure 4.3a). However, during the years of drought and the year following, variability in aspen stem C increment increased markedly. Further analysis of various climate variables impact on stem C increment is recommended to help determine what factors are influencing the inter-annual variability in the aspen and jack pine stem C increments.

4.4.2 Inter-annual Variability in Carbon Storage Estimates

Ecosystem C storage increment estimates (i.e. NEP) from the eddy-covariance system were quite variable from year-to-year, similar to the inter-annual variability in stem biomass. Inter-annual climate variability is recognized as the major factor influencing annual NEP. Often it is the differential effects of climatic variability on GEP and ecosystem respiration (R) that contribute to the significant inter-annual variability in NEP (Barr et al., 2007; Krishnan et al., 2006; Kljun et al., 2006; Barr et al., 2004; Arain et al., 2002; Griffis et al., 2003; Black et al., 2000).

Long-term studies at the OA site have shown that inter-annual differences in NEP were related mainly to differences in leaf phenology and leaf area index (LAI)

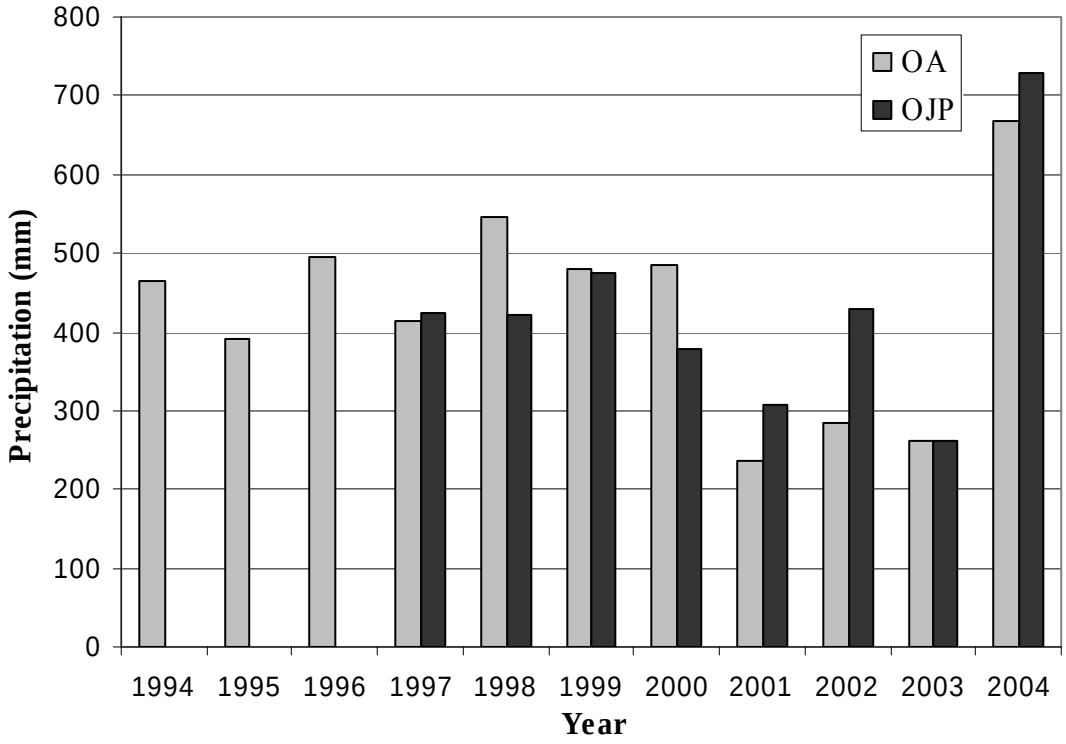

Figure 4.5 Annual cumulative precipitation (mm) at Old Aspen (OA) and Old Jack Pine (OJP). (data provided from the Boreal Ecosystem Research and Monitoring Sites (BERMS) data archive, Environment Canada).

(Barr et al., 2004). Barr et al. (2007) concluded that the timing of leaf emergence is a major determinant of NEP in boreal and temperate deciduous forests via its effect on GEP. The earlier leaves can actively start to photosynthesize C, the greater the amount of C absorbed in the growing season. Respiration was found to be less variable among years than NEP and GEP (Barr et al., 2007). In years of severe drought, the response of R and GEP to reduced soil moisture varied among years. In 2001, drought suppressed R while having little effect on GEP, causing NEP to increase (Barr et al., 2007). In the following years, 2002 and 2003, drought suppressed both R and GEP, resulting in average NEP. The negative NEP recorded in 2004 was a result of the shortest growing season recorded, lowest full-leaf LAI and the slower recovery of GEP to drought compared to R (Krishnan et al., 2006).

The drought of 2001-2003 also dominated the time series at OJP, which consists of only five years total (2000-2004). The greater severity of this drought at OA (Figure 4.5) may explain the greater variability in GEP at OA compared to OJP (Figure 4.3b). As a result of these different drought patterns, OJP was less affected by the drought than OA. This is also reflected in annual NEP at OJP remaining relatively unchanged over the time series. Furthermore, jack pine is considered to be adapted to low soil moisture conditions. The coarse soil texture at this site and large tap root allow these trees to access deeper water reserves, and this may help mitigate the impact of drought.

4.4.3 Convergence of Stem Biomass and Carbon Storage Estimates

There is a strong positive relationship between stem biomass C increment and annual GEP at OA between 1994 and 2004 (Figure 4.2a). The high r^2 value (0.72) indicates that the inter-annual variability in GEP explains 72% of the variability in stem

biomass increment at this site. However, different factors appear to be affecting tree growth and GEP. The inter-annual variation in GEP was strongly influenced by the timing of aspen leaf emergence, which in turn was closely related to spring temperatures (Barr et al., 2004, Black et al., 2000). However, Hogg et al. (2005) found no relationship between aspen stem growth and the estimated date of leaf emergence. Aspen growth was primarily driven by the balance of precipitation to evapotranspiration and insect defoliation (Hogg et al., 2005). The decrease in C uptake in 2001-2003 by both the aspen stem C increment and GEP in response to drought may explain the good agreement between these two variables.

Although the factors affecting stem biomass C increment and GEP are different, the data show that stem biomass C remains a constant fraction of annual GEP. This implies that years with greater photosynthetic activity results in greater stem growth and vise versa. This is particularly true at OA where both the highest and three lowest increments of stem biomass and GEP occurred in the same years, 2001 and 2002-2004, respectively. At OA, stem biomass accounted for 11 ± 2% (±SD) of annual GEP, ranging from 8-13% over the 11-year period, with the lowest allocation in 2003. The reduction of C allocated to the stem in 2003 may be a result of increased allocation belowground during the third year of drought (Landsberg and Gower, 1997).

There is a stronger relationship between stem biomass increment and GEP than with NEP (Figure 4.2b). The lack of relationship to annual NEP can partially be explained by the nature of NEP itself. NEP is the balance of two offsetting processes, GEP and R. Year-to-year changes in annual NEP do not reflect the total story, in terms of the growth of the living biomass. In certain years respiration can be large compared to photosynthesis resulting in negative or near negative NEP (Barr et al., 2007).

Additionally, a substantial fraction of autotrophic respiration occurs outside the growing season making the comparison of annual NEP to stem growth more difficult (Ryan et al., 1997). However, when fall, winter, and early spring respiration are not considered the regression to NEP (April to July period) was significant (Figure 4.1d).

Another important consideration when comparing stem biomass increment to NEP is the inclusion of heterotrophic respiration in the NEP estimate. Heterotrophic respiration has no functional link to stem growth. Therefore, when NEP is incorporated in to the regression the two variables show poor correlation (Figure 4.2b,d; Figure 4.4b,d). Stem growth is related to NEP when only daytime fluxes are considered (Krishnan et al., 2006). Annual daytime NEP was found to have a stronger correlation to stem growth than annual NEP and, according to Krishnan et al. (2006), this is a consequence of the correlation between daytime NEP and photosynthesis (GEP).

At OJP, the lack of significant relationships between stem biomass increment and GEP and NEP is likely due to the short period of flux measurements. The regression analysis was limited to five years greatly restricting the predictive power of the regression. However, even without a large number of years with flux data, it is evident that discrepancies between GEP and stem biomass increment exist (Figure 4.1b). Rocha et al. (2006) also found that photosynthesis and tree ring growth are not necessarily related. They found that tree ring width was uncoupled from previous or current year's carbon uptake at a black spruce stand in Manitoba and hypothesized that ring width may be controlled by something other than photosynthesis alone. The lack of relationship may be due to a large carbohydrate storage reserve in slow growing, stress-tolerant trees (Cannell and Dewar, 1994). Pine species are well known for their stress tolerance and consistently allocate more carbon to their root systems than deciduous

trees (Gower et al., 2001). Ryan et al. (1995) found that the stem generally requires less than 10% of annual GEP to maintain the small fraction of living cells associated with sapwood and phloem. Based on the five years of data available for this study, stem biomass accounted for 10 ± 2% (±SD) of annual GEP, ranging from 8-14% over the 5-year period, with the lowest allocation in 2003. It is unclear whether stem C increment remains a constant fraction of GEP at this site or if during years of stress there was a greater allocation to belowground components.

Lastly, annual stem C increment are slightly underestimated because they are based on trees that were still alive in 2004. A large number of trees at both sites had died during the study period (Section 3.3.1, Table 3.3). Had the trees that died between 1994 and 2004 been accounted for, adding additional biomass to the calculations, the stem C increment would be slightly higher. Based on the assumption that the known number of trees that died by 2004 lived for half the period (i.e. five years), they would have added 0.16 Mg C ha^{-1} and 0.03 Mg C ha^{-1}, at OA and OJP respectively, to the mean annual stem C increment, increasing its value to 1.48 Mg C $ha^{-1}yr^{-1}$ and 0.69 Mg C $ha^{-1}yr^{-1}$, respectively. Accordingly, the regressions between stem C increment and GEP and NEP were stronger when these dying trees were accounted for.

4.4.4 Ten-Year Average Net Primary Productivity

The stem C increment is an important component of the annual NPP budget in forest ecosystems. Although NPP was not measured annually at OA or OJP, all of its components were measured by other researchers between 1994 and 2004. Total average NPP calculated for 1994-2004 was 4.40 Mg C $ha^{-1}yr^{-1}$ and 2.23 Mg C $ha^{-1}yr^{-1}$ at OA and OJP, respectively (Table 4.3). Gower et al. (2001) reported that average total NPP for

Table 4.3 Average annual above- and below-ground net primary productivity (NPP) (Mg C $ha^{-1}yr^{-1}$) by ecosystem component at Old Aspen (OA) and Old Jack Pine (OJP).

Ecosystem Component	Old Aspen			Old Jack Pine		
	Value		Source	Value		Source
	Mg C $ha^{-1}yr^{-1}$			Mg C $ha^{-1}yr^{-1}$		
NPP						
Stem	1.32	(30.0)	allometry this study	0.66	(29.6)	allometry this study
Branches	0.53†	(12.0)	Bernier et al. (2007)	0.32†	(14.3)	Bernier et al. (2007)
New foliage				0.03	(1.3)	allometry this study
Understory	0.53‡	(12.0)	Gower et al. (1997)	0.05‡	(2.2)	Gower et al. (1997)
Coarse roots	0.26§	(5.9)	Pierre Bernier (personal comm.)	0.15	(6.7)	allometry this study
Fine Roots	0.81¶	(18.4)	Kalyn and Van Rees (2006)	0.56¶	(25.1)	Kalyn and Van Rees (2006)
Detritus (foliar litter)	0.95#	(21.6)	Ted Hogg (personal comm.)	0.40††	(17.9)	Jagtar Bhatti (personal comm.)
Other detritus				0.06‡‡	(2.7)	Jagtar Bhatti (personal comm.)
Total aboveground	3.33	(75.7)		1.52	(68.2)	
Total belowground	1.07	(24.3)		0.71	(31.8)	
Total ecosystem	4.40	(100)		2.23	(100)	

Values in parentheses are the contribution of each component to the total ecosystem NPP (%)
† Estimated from foliar litter production multiplied by ratio of branch : foliage production of 0.56 for aspen and 0.86 for jack pine
‡ data from 1994 only
§ based on a coarse root:stem ratio of 0.20
¶ 2-year average (2003, 2004), published values from Kalyn and Van Rees (2006), revised by P. Bernier (personal communication) who noted a calculation error in the published values
#10-year average litterfall (1994, 1996-2004), litter considered to be 45% C (Gower et al., 1997, 2001)
†† 4-year average annual litterfall (2001-2004)
‡‡ 4-year average cone detritus (2001-2004)

24 boreal forest stands was 4.24 Mg C $ha^{-1}yr^{-1}$ ranging from 0.52 to 8.68 Mg C $ha^{-1}yr^{-1}$. The results from OA and OJP in this study are well within this range. At OA, aboveground NPP from this study is comparable to the Bernier et al. (2007) estimate of 3.0 Mg C $ha^{-1}yr^{-1}$ from 2000-2004 at the same site. Likewise, total NPP from OA and OJP are similar to a 65-year old boreal mixedwood forest in Manitoba (Martin et al., 2005) approximately 500 km northeast of OJP.

The most striking difference between OA and OJP is the allocation of C above- and below-ground. Gower et al. (1997, 2001) found that aboveground NPP (stem, branch, foliage and understory) was consistently larger for deciduous than for evergreen boreal forests in each of the major boreal regions and that result is consistent with results from OA and OJP between 1994 and 2004. Conversely, a greater percentage of total NPP is allocated to root production in boreal coniferous than deciduous forests (Gower et al., 1997; Kalyn and Van Rees, 2006). It is clear from the large contribution of fine roots to total NPP, 18% and 25% at OA and OJP respectively, that fine root production must be included to construct complete C budgets for boreal forests (Gower et al., 1997).

Stem growth was the largest contributor to total NPP accounting for 30% at both OA and OJP. Similarly, Bond-Lamberty et al. (2004) reported that wood NPP (stem + branch) accounted for 25.5% of total NPP at a 74-year old well drained black spruce site. Gower et al. (2001) found that wood NPP accounted for 41% of total NPP at variety of boreal forest sites in North America, Europe and Asia. They include 1994 data from OA and OJP (Gower et al., 1997) in their summary and report a contribution of wood NPP to total NPP of 45% and 29% at OA and OJP, respectively. The estimates of wood NPP from Gower et al. (1997), made nearly a decade ago using different

allometric equations, are similar to those in this study. Wood NPP (stem + branch) values in this study were 1.85 and 0.98 Mg C $ha^{-1}yr^{-1}$ at OA and OJP, respectively, whereas Gower et al. (1997) reported an annual wood NPP in 1993 and 1994 of 1.6 and 1.7 Mg C $ha^{-1}yr^{-1}$, respectively at OA, and 0.57 and 0.59 Mg C $ha^{-1}yr^{-1}$, respectively in the same two years at OJP. Moreover, Howard et al. (2004) reports a wood NPP at OJP in both 1999 and 2000 of 0.7 Mg C $ha^{-1}yr^{-1}$.

A critical issue in the forest carbon cycle science is the constancy (or lack of constancy) in the NPP/GEP ratio. NPP results as the difference between GEP and autotrophic respiration (Ra), used for cell maintenance and tissue construction (Ryan et al., 1997). Waring et al. (1998) synthesized data from 12 temperate forest ecosystems in the northern and southern hemispheres and reported a NPP/GEP ratio of 0.47±0.04. The ratio was remarkably consistent among ecosystems. Waring et al. (1998) hypothesized that the consistency of the ratio may be tied to the C/N ratio in plants. Falge et al. (2002) analyzed R and GEP from a variety of FLUXNET research sites around the world and found mean NPP/GEP ratio 0.51 for both temperate coniferous and deciduous forests and 0.48 for boreal evergreen conifers. The results from this study shows NPP/GEP ratios of 0.36 and 0.32 at OA and OJP, respectively. These ratios are low compared to the ratio of 0.47 calculated by Waring et al. (1998). They are similar to the estimate of 0.31 from Ryan et al. (1997) from OA and OJP. The NPP estimates in this study are most likely underestimates because only the live trees that survived the 1994 to 2004 period were included in the stem biomass analysis. If we assume that the trees that died between 1994 and 2004 lived for half the period and include their contribution in the calculation of NPP, total NPP would increase to 4.60 Mg C ha^{-1} yr^{-1} and 2.27 Mg C

ha^{-1} yr^{-1} at OA and OJP respectively, and the NPP/GEP ratios increase to 0.37 at OA and remain unchanged at OJP. There remains considerable uncertainty in estimating NPP in the non-stem components and the comparatively low NPP/GEP ratios reported in this study highlight the need for greater understanding of carbon allocation patterns, particularly belowground.

4.5 Summary and Conclusions

Stem C increments and eddy-covariance measurements of GEP and NEP at OA and OJP showed considerable year-to-year variability between 1994 and 2004. At OA, inter-annual variability in GEP was positively correlated (r^2 = 0.72) with inter-annual variation in stem C increment. Additionally, this study found a positive correlation between growing season GEP and stem C increment. The strong relationships at this site between stem C and photosynthesis provides some confidence that the eddy-covariance system can detect year-to-year changes in the living biomass. In contrast, no significant relationships between stem biomass and GEP or NEP were found at OJP. The lack of strong relationships at OJP may be largely an artifact of the relatively shorter period of eddy-covariance measurements at this site, and additional years of flux measurements would certainly help to understand the inter-annual variations in flux data as they relate to stem C increments.

Between 1994 and 2004, at both OA and OJP, stem C increment remained a constant fraction of GEP between years and a variety of climatic conditions, 11±2% and 10±2%, respectively. This implies that years with greater photosynthesis result in greater stem C increments and vise versa. In this study, stem C increment (or stem NPP) accounted for 30% of total NPP at OA and OJP and is similar to values reported for

other boreal forests. It is clear that when calculating NPP or the NPP/GEP ratio it is important to include belowground pools, particularly fine roots, which can account for a large proportion of annual NPP and easily affect values of total NPP.

Research into the NPP/GEP ratios of various forest ecosystems has focused on trying to find common relationships among plant species around the world. The data in this study show NPP/GEP ratios of 0.36 and 0.32 at OA and OJP, respectively. These results are low relative to other studies from around the world, however most studies have focused on temperate forests. If the boreal forest exhibits different patterns of carbon use efficiency it would be unfeasible to use a single NPP/GEP ratio for all forests. However, if the NPP/GEP ratio is constant across different locations and species and assuming that eddy-covariance systems are giving accurate results of GEP, the use of this ratio will help reduce the difficulty in calculating NPP from GEP (Waring et al., 1998). In the future, complete annual NPP budgets, along with ongoing eddy-covariance measurements could help verify the NPP/GEP ratios presented in this study.

Old aspen and OJP represent two of the dominant upland forest types in the southern boreal forest in Canada. The strong correlation between stem C increments at OA and OJP suggests stem growth at these sites was responding in similar ways to a variety of growing conditions, likewise for annual GEP. Although aspen stem growth appeared to be more affected by drought than jack pine, the spatial variation in the severity of the drought between the two sites likely had a strong impact on the observed responses. Further analysis of various climate variables and their impact on both stem C increment and carbon fluxes across a wider range of forest types may help determine

what factors are most important in governing inter-annual variation in forest growth and carbon cycling at the regional scale.

4.6 Literature Cited

Arain, M.A., T.A. Black, A.G. Barr, P.G. Jarvis, J.M. Massheder, D.L. Verseghy, and Z. Nesic. 2002. Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. Can. J. For. Res. 32: 878-891.

Barr, A.G., T.A. Black, E.H. Hogg, N. Kljun, K. Morgenstern, and Z. Nesic. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. 126: 237-255.

Barr, A.G., T.A. Black, E.H. Hogg, T.J. Griffis, A.D. Theede, N. Kljun, K. Morgenstern, and Z. Nesic. 2007. Climate controls on the carbon and water balances of a boreal aspen forest, 1994-2003. Global Change Biol. 13: 561-576.

Bernier, P.Y. M.B. Lavigne, E.H. Hogg and J.A. Trofymow. 2007. Estimating branch production in aspen, Douglas fir, jack pine, black spruce and balsam fir. Can. J. For. Res. (in press).

Black, T.A., W.J. Chen, A.G. Barr, M.A. Arain, Z. Chen, Z. Nesic, E.H. Hogg, H.H. Nuemann, and P.C. Yang. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophys. Res. Lett. 27: 1271-1274.

Bond-Lamberty, B., C. Wang, and S.T. Gower. 2002. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Global Change Biol. 10: 473-487.

Cannell, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modeling. Adv. Ecol. Res. 25: 60-104.

Dunn, A.L., C.C. Barford, S.C. Wofsy. 2007. A long-term record of carbon exchange in a boreal black spruce forest: means responses to interannual variability, and long-term trends. Global Change Biol. 13: 577-590.

Falge E., D. Baldocchi, J. Tenhunen, M.Aubinet; P. Bakwin, P. Berbigier, C. Bernhofer, G. Burba, R. Clement, K.J. Davis, J.A. Elbers, A.H. Goldstein, A. Grelle, A. Granier, J. Guomundsson, D. Hollinger, A.S. Kowalski, G. Katul, B.E. Law , Y. Malhi, T. Meyers, R.K. Monson, J.W. Munger, W. Oechel, K.T. Paw U, K. Pilegaard, U. Rannik, C. Rebmann, A. Suyker, R. Valentini, K. Wilson, S. Wofsy. 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. For. Meteorol. 113: 53-74.

Gough, C.M., C.S. Vogel, H.P. Schmid, H-B. Su and P.S. Curtis. 2007. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. For. Meteorol. (in press).

Goulden, M.L., J.W. Munger, S-M. Fan. 1996. Exchange of carbon dioxide by a deciduous forest: response to inter-annual climate variability. Science 271: 1576-1578.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele, and T.K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102: 29,029-29,041.

Gower S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder and C. Wano. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl. 11: 1395-1411.

Griffis, T.J., T.A. Black, K. Morgenstern, A.G. Barr, Z. Nesic, G.B. Drewitt, D. Gaumont-Guay, and J.H. McCaughey. 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. Agric. For. Meteorol. 117: 53-71.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can. J. of For. Res. 35: 610-622.

Howard, E.A., S.T. Gower, J.A. Foley and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Global Change Biol. 10: 1-18.

Kalyn, A.L. and K.C.J. Van Rees. 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. 140: 236-243.

Kljun, N., T.A. Black, T.J. Griffis, A.G. Barr, D. Gaumont-Guay, K. Morgenstern, J.H. McCaughey, Z. Nesic. 2006. Response of net ecosystem productivity of three boreal forest stands to drought. Ecosystems 9: 1128-1144.

Krishnan, P., T.A. Black, N.J. Grant, A.G. Barr, E.H. Hogg, R.S. Jassal, and K. Morgenstern. 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. Agric. For. Meteorol. 139: 208-223.

Lambert, M.-C., C.-H. Ung, and R. Raulier. 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. 35: 1996-2018.

Landsberg, J.J., and S.T. Gower. 1997. Applications of physiological ecology to forest management. Academic Press. Toronto.

Martin, J.L., S.T. Gower, J. Plaut and B. Holmes. 2005. Carbon pools in a boreal mixedwood logging chronosequence. Global Change Biol. 11: 1883-1894.

Matthews, G. 1993. The carbon content of trees. Forestry Commission, Technical Paper 4. Forestry Commission, Edinburgh.

Rocha, A.V., M.L. Goulden, A.L. Dunn and S.C. Wofsy. 2006. On linking interannual tree ring variability with observations of whole-forest CO_2 flux. Global Change Biol. 12: 1378-1389.

Ryan, M.G., S.T. Gower, R.M Hubbard, R.H. Waring, H.L. Gholz, W.P. Cropper and S.W. Running. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101: 133-140.

Ryan, M.G., M.B. Lavigne, and S.T. Gower. 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J. Geophys. Res. 102: 28,871-28,883.

Waring, R.H., J.J. Landsberg and M. Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18: 129-134.

Zweifel, R., L. Zimmerman, F. Zeugin, and D.M. Newbery. 2006. Intra-annual radial growth and water relations of trees: implications toward a growth mechanism. J. Exp. Bot. 57: 1445-1459.

5. GENERAL DISCUSSION AND CONCLUSIONS

Carbon (C) has become a very important element in recent decades, scientifically, economically and increasingly, politically. The amount of C present in the air, land and ocean has preoccupied many scientists for many years. Increasing atmospheric carbon dioxide (CO_2) concentrations have driven the need to learn more about the interactions between the C in the atmosphere and the other parts of the global C cycle. Because plants use CO_2 in photosynthesis, they have become the focus of much research as a way to mitigate increasing atmospheric concentrations of CO_2. From a global perspective, forests store huge amounts of C with the potential to hold more. The boreal forest is one of the largest forest biomes and whether forests are C sinks or C sources has become an important question.

The goals of this project were: to estimate the total change in ecosystem C over a 10-year period in two representative boreal forest stands, and to evaluate the year-to-year changes in C uptake. The results from this study showed generally good agreement between 10-year eddy-covariance and biometric C stock change estimates from 1994 to 2004. Using both approaches, the total change in ecosystem C was positive in both the aspen and jack pine stands and the increases were comparable between methods. This general consistency between biometric and eddy-covariance estimates suggests that some confidence can be placed in both approaches, despite inherent, but not easily quantifiable uncertainties. These uncertainties make any validations of one approach

over another difficult and resolving these uncertainties is an important issue deserving future work.

There are tremendous benefits to completing two independent assessments of the forest C balance. Unlike the eddy-covariance method, which measures the net change in total ecosystem C stocks, the biometric approach provides detailed information about which component C stocks are changing. The results from this study showed that, while both sites were sinks of C between 1994 and 2004, the dominant stock changes occurred in different C pools - the forest floor at OA and in the living vegetation at OJP. While the living trees at OA, a relatively mature aspen stand, actively sequestered C over the decade of interest, an equal amount of C was lost from this pool through the death and falldown of many trees, resulting in the large increase of C in the detrital pools. In contrast, the living biomass at OJP seemed to be influenced to a lesser extent by tree mortality and falldown rates and as a result increased substantially in its total jack pine C stock.

The second objective of this project was to investigate the inter-annual variability in C uptake in these two forested stands. This was accomplished by measuring the inter-annual variability in the live stem biomass C increment at OA and OJP, and comparing the stem C increment with annual and growing season gross ecosystem photosynthesis (GEP) and net C exchange (net ecosystem productivity, NEP) as measured by eddy-covariance.

As expected, stem C increments and eddy-covariance measurements of GEP and NEP at OA and OJP showed considerable year-to-year variability between 1994 and 2004. At OA, this study found a significant positive correlation between GEP and stem

biomass C increment. No significant relationships between stem biomass C and GEP or NEP were found at OJP. The strong relationship at OA between stem biomass C and photosynthesis provides some confidence in the eddy-covariance system that it can detect year-to-year changes in the living biomass, while the lack of strong relationships at OJP is likely due to the limited number of eddy-covariance measurement years at this site. At OJP, the regression analysis was limited to five years, greatly restricting its statistical robustness. Additional years of flux measurements would certainly help to understand the inter-annual variations in NEP and GEP as they relate to stem C increments.

The stem C increment is an important component of the annual NPP budget in forest ecosystems. Stem C increment made the largest contribution to total NPP between 1994 and 2004 at both OA and OJP. At both sites, aboveground components accounted for a greater percentage of NPP compared to belowground components. However, allocation belowground was greater at the jack pine site. The NPP/GEP ratios from this project indicate a higher cost of production compared to more temperate species. At OA, for every unit of photosynthesis absorbed, 36% became part of the trees component parts, whereas 64% was lost through autotrophic respiration. These results are in contrast with other studies that suggest a constant NPP/GEP ratio of ~45% across different locations and species. That said, there remains considerable uncertainty in estimating the non-stem components of NPP. The relatively low NPP/GEP ratios reported in this study highlight the need for greater understanding of carbon allocation patterns.

The quantification of NPP and NEP between 1994 and 2004 proved to be quite challenging. The long sampling interval in this study made it easier to detect changes in each ecosystem component but data availability from previous work at both sites became more difficult. The 10-year change in ecosystem components relied on previously published data on these two ecosystems from the summer of 1994. In many cases, the published results included only average values limiting statistical analyses. Certainly, the lack of detailed soil data from the 1994 sampling made the analysis of soil C stock changes more difficult. However, large scale research projects, like BERMS and the FCRN, have extensive data archives which should improve data access for future studies. Eddy-covariance measurements continue to be made at both sites and an effort should be made to repeat biometric measurements at OA and OJP every five years to further reduce any uncertainties in the total ecosystem C stocks. The quantification of total ecosystem C stocks and C stock changes should remain a priority alongside eddy-covariance flux measurements.

6. APPENDICES

APPENDIX A

Plot locations

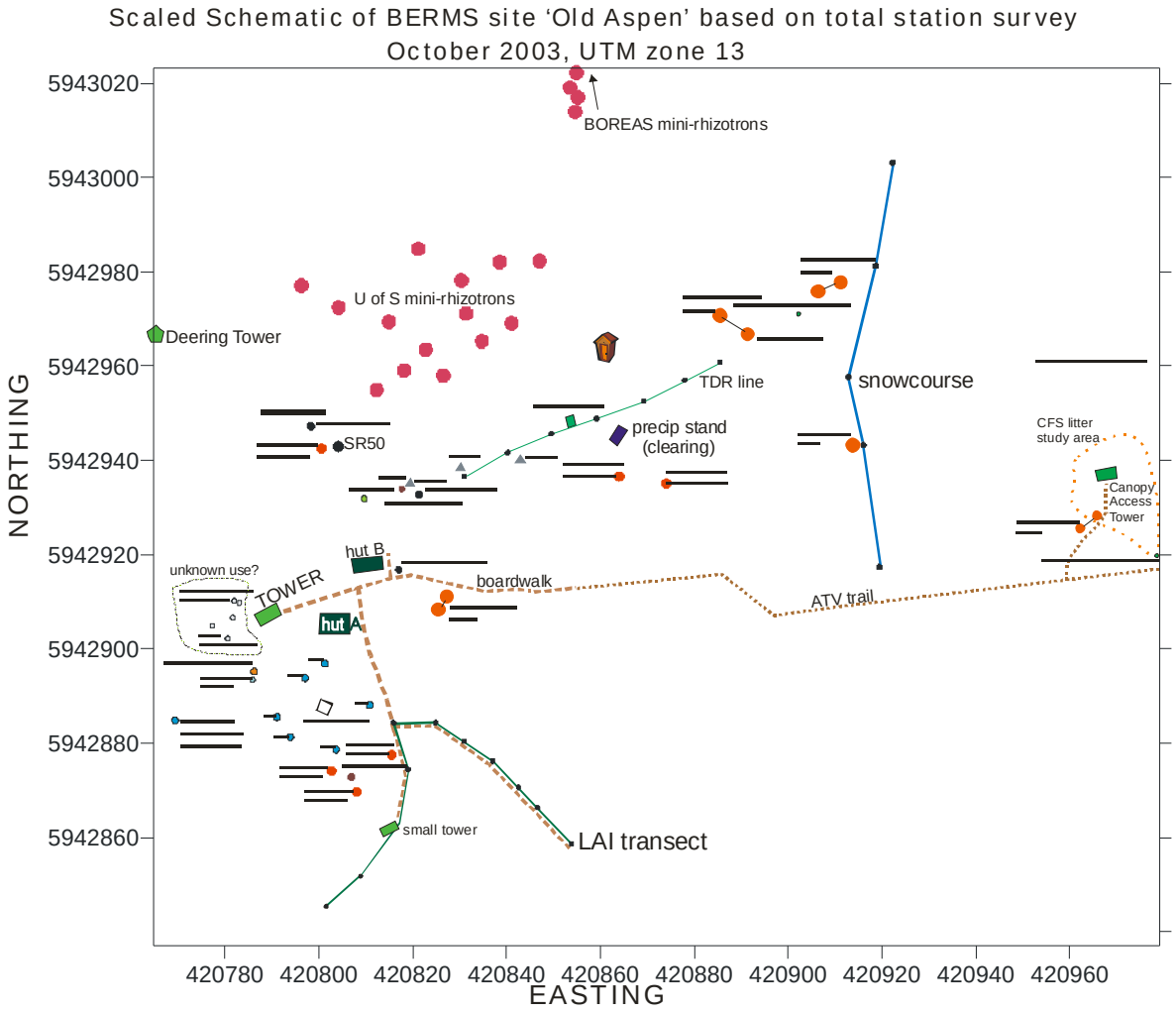

Figure A.1 Scaled diagram of Old Aspen (OA). Gower et al. (1997) plots used in this study located alongside the BOREAS mini-rhizotrons with one plot located north and east of the U of S mini-rhizotrons and deering tower. Fournier et al. (1997) plot located approximately 50-100m south west of the main instrument tower.

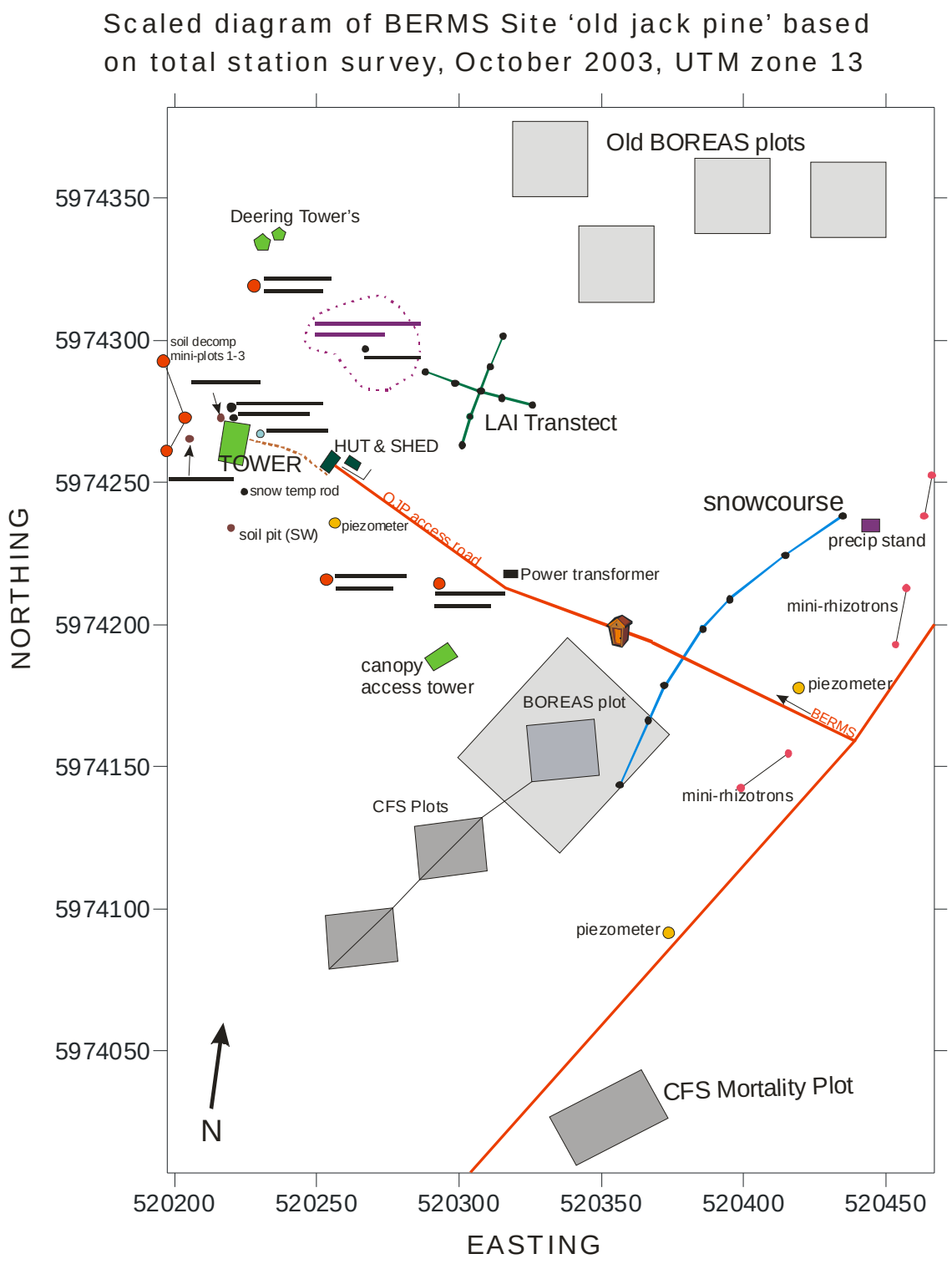

Figure A.2 Scaled diagram of Old Jack Pine (OJP). Gower et al. (1997) plots used in this study located north east of the LAI transect labelled as "Old BOREAS plots". Fournier et al. (1997) plot located south of access road labelled "BOREAS plot".

APPENDIX B

Plot level coarse woody debris data

Table B.1 Woody debris plot summary at Old Aspen (OA) measured in July 2004.

	Diameter class (cm)					
Woody debris	< 0.5	0.5-<1.0	1.0-<3.0	3.0-<5.0	>5.0	Total
Plot 1†						
intersections	76	45	40	5	29	
volume	0.64	0.99	3.40	1.59	86.91	93.52
mass	0.34	0.45	1.49	0.67	31.70	34.65
carbon	0.17	0.23	0.75	0.33	15.85	**17.33**
Plot 2						
intersections	58	52	41	10	33	
volume	0.49	1.14	3.48	3.18	53.20	61.49
mass	0.26	0.52	1.53	1.33	18.42	22.07
carbon	0.13	0.26	0.77	0.67	9.21	**11.03**
Plot 3						
intersections	42	40	30	12	36	
volume	0.35	0.88	2.55	3.81	65.15	72.74
mass	0.19	0.40	1.12	1.60	22.96	26.27
carbon	0.09	0.20	0.56	0.80	11.48	**13.14**
Fournier Plot‡						
intersections	122	116	65	11	66	
volume	0.51	1.27	2.76	1.75	58.34	64.63
mass	0.27	0.58	1.21	0.73	20.15	22.96
carbon	0.14	0.29	0.61	0.37	10.08	**11.48**

† Plot 1-3: total transect length was 75m

‡ Fournier Plot: total transect length was 150m

Table B.2 Woody debris plot summary at Old Jack Pine (OJP) measured in July 2004.

	Diameter class (cm)					
Woody debris	< 0.5	0.5-<1.0	1.0-<3.0	3.0-<5.0	>5.0	Total
Plot 2†						
intersections	59	22	16	11	13	
volume	0.50	0.48	1.36	3.49	12.61	18.44
mass	0.26	0.21	0.57	1.47	4.57	7.08
carbon	0.13	0.11	0.29	0.73	2.29	**3.54**
Plot 3						
intersections	65	25	6	9	13	
volume	0.55	0.55	0.51	2.86	15.44	19.90
mass	0.29	0.24	0.21	1.20	5.61	7.55
carbon	0.15	0.12	0.11	0.60	2.80	**3.78**
Plot 4						
intersections	52	29	14	6	17	
volume	0.44	0.64	1.19	1.91	13.99	18.16
mass	0.23	0.28	0.50	0.80	5.15	6.96
carbon	0.12	0.14	0.25	0.40	2.57	**3.48**
Fournier Plot‡						
intersections	102	29	21	18	16	
volume	0.43	0.32	0.89	2.86	5.77	10.27
mass	0.23	0.14	0.37	1.20	2.12	4.07
carbon	0.11	0.07	0.19	0.60	1.06	**2.03**

† Plot 2-3: total transect length was 75m, plot 1 not sampled

‡ Fournier Plot: total transect length was 150m

APPENDIX C

Plot level mineral soil and forest floor C content

Table C.1 Plot level forest floor (LFH) and mineral soil carbon content at Old Aspen (OA) sampled in July 2004.

	Plot 1	Plot 2	Plot 3
		Mg C ha^{-1}	
Old Aspen			
Forest floor†	30.2	31.2	40.5
Mineral soil‡	36.8	33.2	39.3

† Forest floor total includes both the LFH and Ah horizons.
‡ Calculated to a depth of 70cm below the soil surface

Table C.2 Plot level forest floor (LFH) and mineral soil carbon content at Old Jack Pine (OJP) sampled in September 2004.

	Plot 1	Plot 2	Plot 3
		Mg C ha^{-1}	
Old Jack Pine			
Forest floor†	6.1	8.4	9.6
Mineral soil‡	15.5	15.8	17.2

† Forest floor total includes lichen/bryophytes on the soil surface and fine woody debris
‡ Calculated to a depth of 70cm below the soil surface

APPENDIX D

Plot level biomass C estimates

Table D.1 Biomass carbon estimated from Lambert et al. (2005) allometric equations in the Gower et al. (1997) plots at Old Aspen (OA).

Ecosystem Component	Plot 1		Plot 2		Plot 3	
	1994	2004	1994	2004	1994	2004
	Mg C ha^{-1}					
Living vegetation						
Stem	60.2	56.5	55.5	59.7	85.3	83.4
Branches	7.5	6.4	6.9	6.8	10.8	9.6
Foliage	1.5	1.3	1.4	1.4	1.9	1.6
Coarse roots†	8.9	7.9	8.3	8.4	11.7	10.7
Detritus						
Standing dead	9.3	4.3	9.6	6.5	6.7	7.5
Coarse roots†	1.3	0.6	1.5	0.9	1.0	1.0
Total	88.8	77.1	83.6	83.6	117.3	113.8

† Allometric equations from Ruark and Bockheim (1987).

Table D.2 Biomass C estimated from Lambert et al. (2005) allometric equations in the Gower et al. (1997) plots at Old Jack Pine (OJP).

Ecosystem Component	Plot 2†		Plot 3		Plot 4	
	1994	2004	1994	2004	1994	2004
	Mg C ha^{-1}					
Living vegetation						
Stem	20.1	24.6	27.8	32.6	31.3	37.1
Branches	1.9	2.3	2.6	3.1	2.9	3.5
Foliage	1.5	1.6	1.9	2.0	2.1	2.3
Coarse roots†	4.1	5.1	5.7	6.8	6.4	7.7
Detritus						
Standing dead	6.6	5.1	8.5	7.5	4.7	3.3
Coarse roots†	1.2	0.9	1.5	1.4	0.8	0.6
Total	35.3	39.6	48.0	53.4	48.3	54.5

† Plot 1 not included in the analysis

‡ Allometric equations from Steele et al. (1997, unpublished data).

Table D.3 Plot level understory biomass carbon content at Old Aspen (OA) measured in July 2004.

	Plot 1	Plot 2	Plot 3
		Mg C ha^{-1}	
Understory vegetation			
Branches	2.6	1.8	4.1
Foliage	0.46	0.31	0.59
Annual herbs	0.12	0.02	0.03
Lichen/Bryophytes	-	-	-
Total	3.2	2.1	4.8

Table D.4 Plot level understory biomass carbon content at Old Jack Pine (OJP) measured in September 2004.

	Plot 2	Plot 3	Plot 4
		Mg C ha^{-1}	
Understory vegetation			
Branches	-	-	-
Foliage	-	-	-
Annual herbs	0.11	0.10	0.20
Lichen/Bryophytes†	-	-	-
Total	3.2	2.1	4.8

† sampled with forest floor

APPENDIX E

Understory Vegetation Cover

Table E.1 List of species and their relative proportion to total understory vegetation at Old Aspen (OA) measured in September 2004.

Species	Relative Proportion†
	%
beaked hazelnut‡	66
prickly rose	15
dewberry	13
Western Canada violet	9
creamy pea vine	5
bunchberry‡	5
grass‡	5
cranberry	4
wild red raspberry	3
northern bedstraw	3
palmate leaved colts foot	3
common pink wintergreen	3
lily of the valley‡	3
wild strawberry	2
bishops cap	2
wild sasparilla	2
fairy bells	trace
sweet scented bedstraw	trace
aster	trace

† Relative proportion based on mean calculated from 5 vegetation clip plots.
‡ Species found in each plot

Table E.2 List of species and their relative proportion to total understory vegetation at Old Jack Pine (OJP) measured in September 2004.

Species	Relative Proportion†
	%
green reindeer lichen‡	63
common bearberry	13
grey reindeer lichen‡	13
northern reindeer lichen	10
sphagnum moss	10
lingon berry	10
prickle cladonia	8
brown pixie cup	5
fungus	5
horn cladonia	3
frog's pelt	3
mealy primrose	3
smooth fleabane	3
mushrooms	2
buttercup family	2
awned hair cap	2
green wintergreen	2
wild lilly of the valley	1
snowberry	1
water birch	1
jack pine saplings	1
shrub funnel lichen	trace
brown foot cladonia	trace
tiny toothpick cladonia	trace
ribbed cladonia	trace
false pixie cup	trace
red pixie cup	trace
sulphur cup	trace
grass	trace
hairy screw moss	trace
fragile screw moss	trace
tall clustered thread moss	trace

† Relative proportion based on mean calculated from12 vegetation clip plots
‡ Species found in each plot